CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 16 MARCH 1972

CONTRIBUTIONS IN MARINE SCIENCE

VOLUME 16, MARCH, 1972

PUBLISHED BY

THE UNIVERSITY OF TEXAS
MARINE SCIENCE INSTITUTE

at

PORT ARANSAS, TEXAS

Editor: Martin Sage

Technical Editor: Mrs. Ruth Grundy

CONTRIBUTIONS IN MARINE SCIENCE (formerly *Publications of the Institute of Marine Science*) is printed at irregular intervals by The University of Texas and includes papers of basic or regional importance, in marine sciences, with emphasis on the Gulf of Mexico and surrounding areas.

Issues are distributed at a cost of $4.15 per copy (no discounts possible), or on an exchange basis.

Reprints of individual articles are distributed through the authors only.

For orders (Volumes 6 onward plus one supplement are available), further information, or exchange arrangements, please write to the Librarian, The University of Texas Marine Science Instiute at Port Aransas, Texas 78373. Intending contributors should consult the Instructions to Authors included in this volume.

Contents

Fishes Associated with the Pelagic Sargassum Complex, with a Discussion of the Sargassum Community. *James K. Dooley* 1

Developmental Osteology of the Lined Sole, *Achirus lineatus* (Pisces: soleidae). *Charles R. Futch, Robert W. Topp,* and *Edward D. Houde*..... 33

Diurnal Variation in Fattening Response to Prolactin Treatment in Two Cyprinodontid Fishes, *Cyprinodon variegatus* and *Fundulus similis*. *Victor L. deVlaming* and *Martin Sage* 59

Spray-marking Juvenile Shrimp with Granular Flourescent Pigment. *Robert C. Benton* and *Donald Lightner*..... 65

Growth and Seasonal Distribution of the Elasmobranch *Dasyatis sabina*. *M. Sage, R. G. Jackson, W. L. Klesch,* and *V. L. deVlaming*..... 71

Notes on Distribution, Size, and Ovarian Development of some Penaeid Shrimps in the Northwestern Gulf of Mexico, 1961–62. *Harold A. Brusher, William C. Renfro,* and *Richard A. Neal*..... 75

Beach Changes on the Central Texas Coast associated with Hurricane Fern, September, 1971. *Richard A. Davis, Jr*..... 89

Silica Contents in the Northwestern Florida Gulf Coast. *Carol F. Stephens* and *Carl H. Oppenheimer* 99

The Distribution of Dissolved Organic Matter in the Near-Shore Waters of the Texas Coast. *Larry G. Maurer* and *P. L. Parker*..... 109

Size-related Metabolic Responses of the Pinfish, *Lagodon rhomboides*, to Salinity Variations and Sublethal Petrochemical Pollution. *Thomas C. Kloth* and *Donald E. Wohlschlag*..... 125

Stable Carbon Isotope Ratio Variations in the Organic Carbon from Gulf of Mexico Sediments. *P. L. Parker, E. Wm. Behrens, John A. Calder,* and *David Shultz* 139

Lipid Geochemistry of a Mississippi Coastal Bog Environment. *Julia R. Sever, Thomas F. Lytle,* and *Pat Haug* 149

Marsh Production: A Summary of the Literature. *Carolyn W. Keefe*..... 163

Instructions to Authors 182

FISHES ASSSOCIATED WITH THE PELAGIC SARGASSUM COMPLEX, WITH A DISCUSSION OF THE SARGASSUM COMMUNITY[1]

James K. Dooley[2]

Department of Zoology, University of South Florida, Tampa, Florida 33620

ABSTRACT

From April 1966 through May 1967, some 3,200 kgm (3.5 tons) of sargassum were collected in the Florida Current. Analysis revealed approximately 8,400 fishes belonging to 8 orders, 23 families, 36 genera and 54 species. The families Carangidae (14 species), Monacanthidae (10 species), Balistidae (4 species) and Antennariidae (1 species) numerically comprised 90% of all fishes collected. Sargassum was present in very low quantities in spring and winter, while tremendous quantities were available in summer and fall. Summer and fall were marked by fewer, larger fishes than winter and spring. As a consequence of surface current patterns, sargassum acts as a vehicle for dispersal of some of its inhabitants. The sargassum community appears to be important in the life histories of many species of pelagic, littoral and benthic fishes, providing them with a substratum, protection against predation and concentration of food in the open sea.

INTRODUCTION

This study concerns the fishes of the pelagic sargassum complex in the Florida Current, including their seasonal occurrence, relative abundance and ecological relationships. The role of sargassum during the ontogeny of the fifty-four species collected in this study is also discussed. In addition, a brief consideration of the North Atlantic sargassum community and its biogeographical distribution is included.

Columbus referred to the drifting weed encountered during his voyage of 1492 and since then the pelagic sargassum complex has been known but not throughly studied. Kuntze (1881) and Krummel (1891) quantitatively surveyed the weed in the Sargasso Sea; Winge (1923) and Parr (1939) studied the distribution of sargassum in the North Atlantic; Deacon (1942) generally discussed the Sargasso Sea; Woodcock (1950) described the buoyancy of sargassum weed; Faller and Woodcock (1964) studied the spacing of sargassum windrows; and Lang-

[1] A portion of a thesis submitted to the faculty of the Graduate School of the University of South Florida, Tampa, Florida in partial fulfillment of the requirements for the degree of Master of Arts, March 1970.

[2] Present address: Department of Zoology, University of North Carolina, Chapel Hill, North Carolina and Institute of Marine Sciences, University of North Carolina, Morehead City, North Carolina 28557.

muir (1938) discovered that sargassum windrows were oriented along the convergencies of circulation cells of the sea surface.

The invertebrate fauna of the sargassum has been examined to some extent. Timmermann (1932) studied the zoogeographical distribution of the invertebrates; Conover and Sieburth (1964) examined the effect of sargassum distribution on its epibiota; Prat (1935), Ekman (1967) and Hedgpeth (1953, 1957) discussed the sargassum community; Burkenroad (1939) studied the hydroids; several epizoic flatworms were described by Hyman (1939); Hackett (1963) compiled a checklist of sargassum fauna and flora; Weis (1968) wrote a brief note on several previously unreported gastropods; and Fine (1970) although hampered by limited sampling examined the diversity and affinity of sargassum fauna off North Carolina.

The Pacific Ocean sargassum complex has been studied extensively by Japanese workers. Kojima (1955, 1956, 1957, 1960, 1960a, 1961, 1966) has written prolifically on the dolphin and its reaction to flotsam. Hirosaki (1960, 1960a, 1963, 1963a, 1964, 1965) studied the ecology and behavior of fishes found under sargassum and other flotsam off Japan. Ida, Hiyama and Kusaka (1967, 1967a) examined weed associated fishes including their behavior and food habits. Imamura, et al. (1965) discussed a raft used to attract dolphins; Senta (1962, 1965, 1966, 1966a, 1966b) attempted to explain factors that caused fishes to associate with floating weed. Shojima and Ueki (1964) and Uchida and Shojima (1958) discussed larval and juvenile fishes found in sargassum; and Yabe and Mori (1950) described the association of tuna and flotsam. Mukai (1971) studied the invertebrates associated with beds of sessile sargassum in the Inland Sea of Japan; and Besednov (1960) collected fishes under central Pacific sargassum patches.

Little work has been done on the relationships of North Atlantic fishes with sargassum weed. However, many of the fishes found with sargassum have been studied such as: Collette (1962) a new halfbeak, Bruun (1935) and Breder (1938) on the flying fishes, Herald (1965) the American pipefishes, Nichols (1937), McKenney, et al. (1958) and Berry (1959) the crevalle jacks (*Caranx*), Mather (1958) the amberjacks (*Seriola*) of the western North Atlantic and Berry (1968) described a new species of Jack (*Decapterus tabl*) found in this study. Gibbs and Collette (1959) and Beardsley (1967) studied the dolphins (*Coryphaena*), Lewis (1967) the food habits of the yellowfin tuna and dolphin, Caldwell (1962) larval and juvenile goatfishes, Moore (1962) the kyphosids, Matsui (1967) the mackeral (*Scomber*), Taning (1961) and Arata (1954) examined the life history of the swordfish (*Xiphias*), Legaspi (1956) and Mckenney (1961) the driftfish (*Psenes*), Anderson (1957) the early development of the silver mullet (*Mugil curema*), Berry and Vogele (1961) the filefishes, Moore (1967) the triggerfishes and Adams (1960) on the life history of the sargassum fish (*Histrio histrio*). Longley and Hildebrand (1941) surveyed the fishes of Tortugas, Florida and mentioned some fishes found with sargassum.

SARGASSUM COMMUNITY

The sargassum community is a world-wide circumtropical phenomenon comprised of a rather unique and diverse association of organisms. Although the

community has faunal affinities with littoral areas and contains some transients from inshore waters the complex is holopelagic. Pelagic sargassum may have evolved from a benthic form in littoral areas of the Caribbean Sea, but age of the community can only be conjectured because of the lack of fossil evidence. The relative age of the community may be estimated by the fact that the only two species of endemic fishes belong to phylogenetically advanced forms.

The sargassum community is a concentration of food in the epipelagia in the area outlined in Figure 1. Upon sinking, pelagic sargassum adds organic carbon to the ocean bottom over broad areas of the North Atlantic and is a source of food for a major constituent of the deep-sea benthos (Schoener and Rowe, 1970). The invertebrate fauna is comprised of approximately 100 species, nearly 10% endemic; major groups include: hydroids, anthozoans, flatworms, bryozoans, polychaetes, gastropods, nudibranchs, bivalves, cephalopods, pycnogonids, isopods, amphipods, copepods, decapod crustaceans, insects and tunicates. Shrimp and crabs comprise the bulk of the invertebrates and a major source of food for sargassum associated fishes. The importance of sargassum in the development of many pelagic fishes and fishes with pelagic stages will be discused in detail.

DISTRIBUTION

Pelagic sargassum occurs in the Atlantic, Pacific and Indian Oceans and the Red Sea (Markkaveeva, 1965). Krummel (1891) estimated that in the North Atlantic, sargassum covered nearly two million square miles; Parr (1939) measured the density of the weed at from two to five tons per square mile (2.6 km^2) of sea surface.

The sargassum complex in the Florida Current study area is comprised of about 80% *Sargassum natans*, 10% *S. fluitans* and 10% detached sessile *S. filapendula*. Fragments of aquatic vascular plants and other debris are ofen found interspersed with sargassum. The two formerly mentioned holopelagic pecies of sargassum are sterile, reproducing vegetatively by fragmentation. The weed maintains its buoyancy by a large number of gas filled vesicles (Woodcock, 1950) and can probably remain afloat idefinitely unless killed by cold temperature (below 18°C), sunk by great wave action or submerged by excessive epibiotic growth (Parr, 1939).

Sargassum circulates between 20° and 40° N. latitude and between 30° W. longitude and the western edge of the Gulf Stream (Timmermann, 1932). Parr (1939) and Conover and Sieburth (1964) found a paucity of weed in the central Caribbean Sea. Some weed occurs in the Gulf of Mexico, apparently carried out of the northern Caribbean between Yucatan and Cuba. Whether the weed is self-sustaining is not known, but the sargassum carried into the Gulf of Mexico is probably lost to the North Atlantic community. Considerable qualities of sargassum are carried between the Bahaman Bank and Cuba, channeled northward through the Straits of Florida by the Florida Current and either remain in the Gulf Stream drift, sink or are blown ashore by strong onshore winds.

The center of distribution of pelagic sargassum appears to be in the vicinity of the North Atlantic gyre southeast of Bermuda between 28° and 34° N. lati-

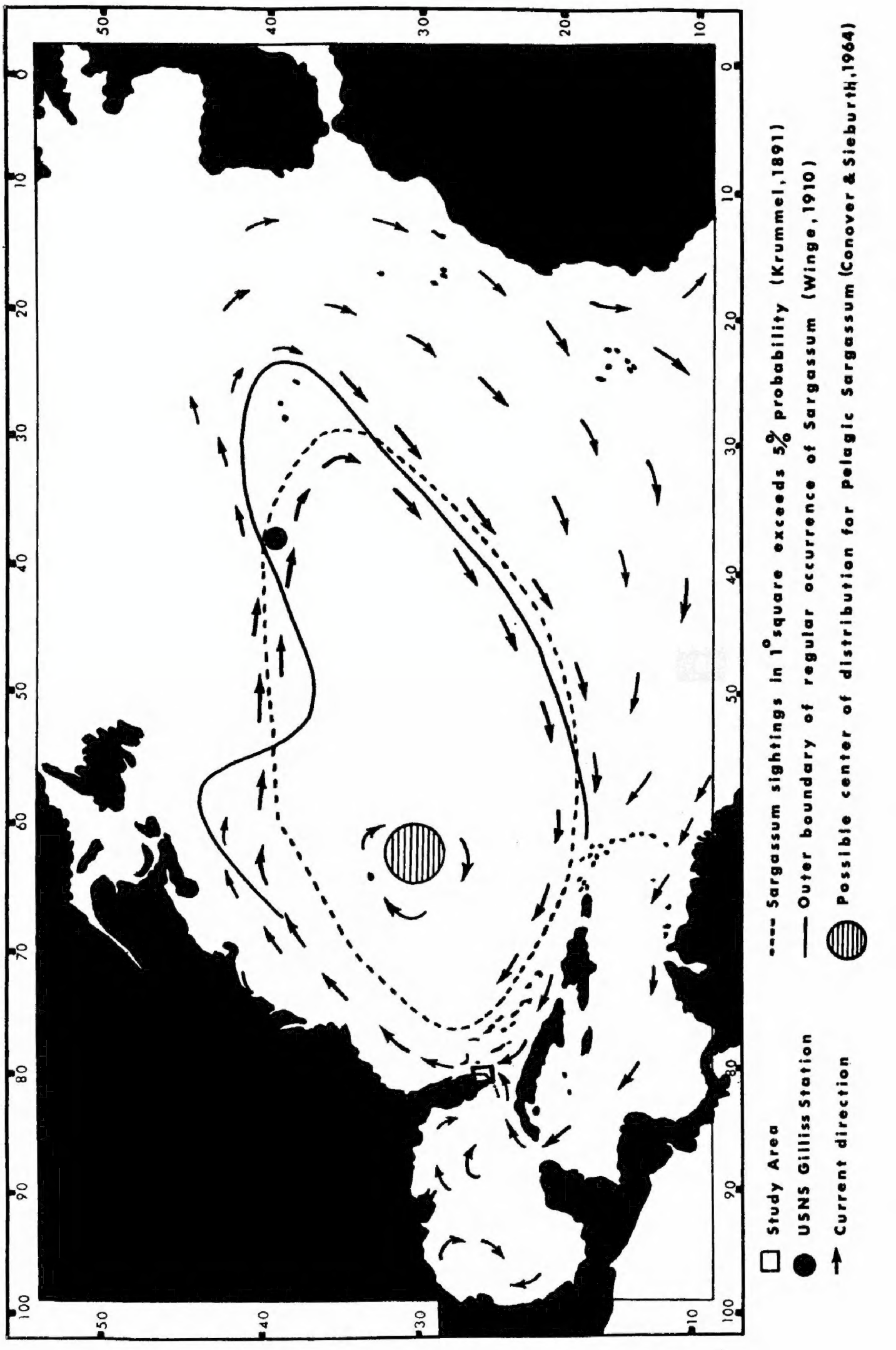

FIG. 1. Outer boundary of regularly occurring pelagic sargassum weed in the North Atlantic, including the possible center of distribution, area of study, and a collection station near the Azores from the vessel USNS Gilliss.

tude and 65° W. longitude (Conover and Sieburth, 1964; Sieburth and Conover, 1965; Fig. 1). According to Winge (1932) the 18° isocryme limited sargassum distribution and Parr (1939) believed that cold winds upon the exposed shoots was a critical factor.

MATERIALS AND METHODS

Sargassum samples were taken within the Florida Current semi-monthly from April 1966 through May 1967. The stations were generally located in an area within a 16 km circle approximately 11 km east southeast off the southern tip of Key Biscayne, Florida (Fig. 2). Several stations were up to 40 km offshore, and two stations were inshore of the Florida Current. The current edge was usually from 1 to 2 km east of the 20 m bottom contour (Fig. 2). The availability and proximity of the sargassum determined the precise sampling location. The amount of weed and the number of stations taken per trip was determined by the time required to sort each sample. Most samples were collected using a miniature purse seine, although a hook and line was used when large fishes were observevd near sargassum. A dip net was occasionally used when the seas were rough and the weed very scattered.

A miniature purse seine was modified from a design by Hunter, Aasted and Mitchell (1966). The net used was rectangular and measured 30.5 m by 5.2 m. The body of the net was constructed from two 61.5 m by 2.6 m panels of blue nylon 12.5 mm stretch mesh sewn together. Two meters of netting were hung on each meter of head rope. The additional netting rendered "bag" to the net and decreased the tendency for the lead line to ascend during pursing operations. The net was lighter and cost less to construct than the seine designed by Hunter, Aasted and Mtichell (1966).

Sampling Technique

A sargassum patch that could be entirely encircled with the seine was selected. The patch was approached from the vessel's starboard side from downwind. A drougue chute was deployed and the net played out. The boat circled the patch in a clockwise direction so that upon completion of the circle the vessel would lie downwind of the net to prevent drifting over the catch. The net was closed and pursed as quickly as possible The entire operation generally took from 30 to 45 minutes.

The sargassum sample was rinsed thoroughly in large tubs and the rinse water strained through a 1mm mesh sieve. The weed was wet weighed to the nearest ½ kg. on a machete beam balance; a one gallon sample of weed was preserved for epibiotic analysis and the remainder discarded. The term sargassum biomass discussed later refers to the fresh wet weight.

Samples were sorted and identified and the numbers and kinds of fishes were recorded. Standard lengths were measured to the nearest mm with dial calipers or dividers. The preserved wet weight of each fish species was determined to the nearest gram with a triple beam balance within a week of its capture. The term fish biomass used later refers to the weight formerly discussed. Only superficial examination of the food habits of some sargassum associated fishes was attempted. Stomach analyses were conducted on preserved specimens of the ten most numerous species of fishes from a range of sizes and from each season of occurrence. Details of the food habits of these fishes will be discussed later. Specimens collected were entered into the museum of N.O.A.A., Tropical Atlantic Biological Laboratory, Miami, Florida.

The location of the sampling station was fixed with a radio directional finder. Field data included the determination of surface salinity (with an optical densitometer), surface and air temperatures, sea state, cloud cover, approximate wind velocity, time of day and characteristics of the sargassum patches.

RESULTS AND DISCUSSION

During the course of this study 3,200 kgm (3.5 tons) of sargassum were collected containing approximately 8,400 fishes belonging to 8 orders, 23 families,

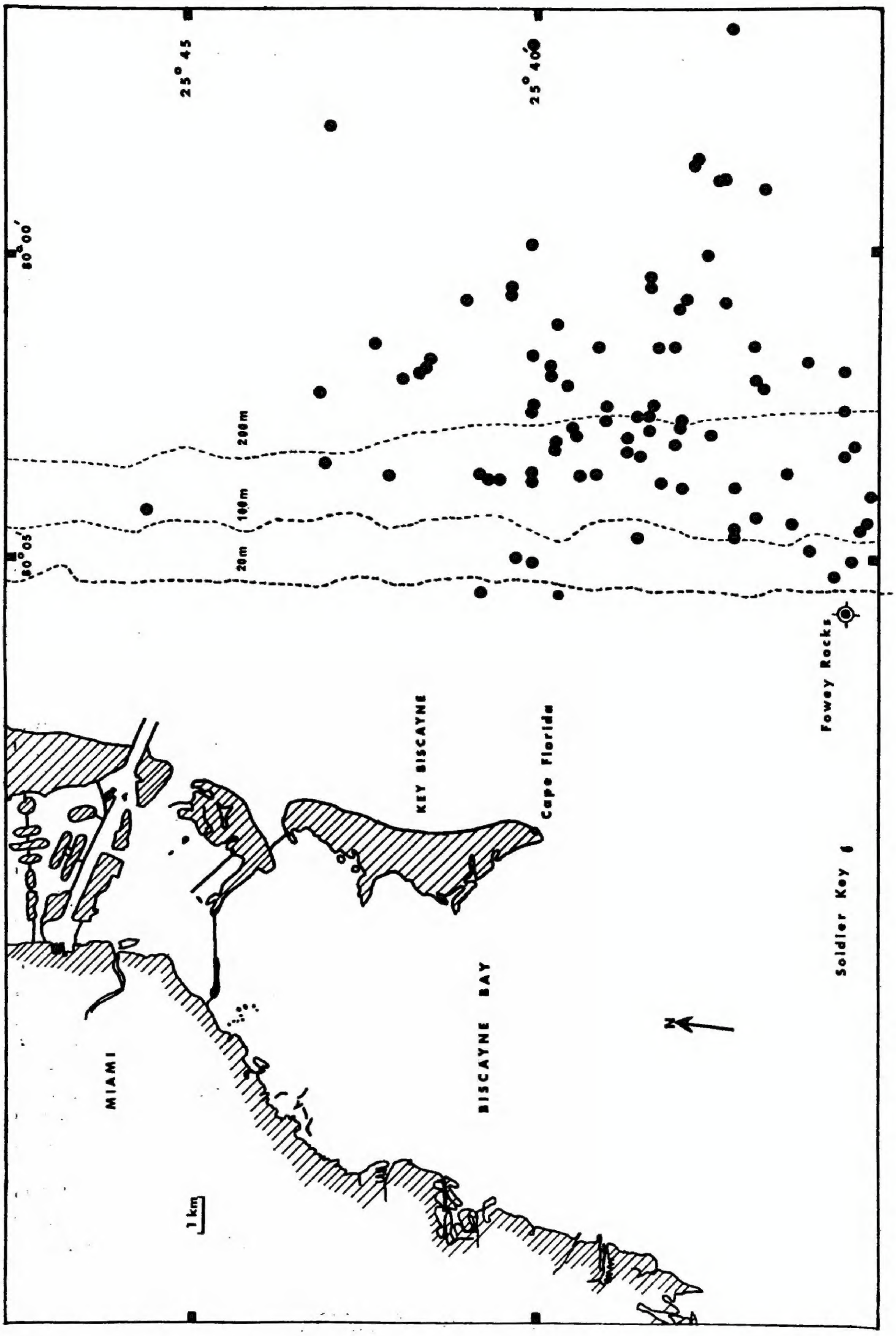

FIG. 2. Area of study and sampling locations. Dots denote station locations. Enclosed dot is Fowey Rocks lighthouse. Dashed lines are approximate bottom contours.

36 genera and 54 species. Statistical analyses revealed a positive correlation between weed biomass and the numbers of the two most numerous species of fishes found in sargassum. The correlation coefficient for *Histrio histrio* was $r = 0.31$ and significantly different from 0 (completely random) at the 0.1% level; for *Stephanolepis hispidus* $r = 0.21$ and significantly different from 0 at the 10% level. Analyses of several other less numerous species of fishes failed to reveal any significant correlation. In addition, no significant correlation was found between the total biomass of fishes and weed, probably due to the high degree of variance introduced by the less numerous species (Fig. 3). June through October was marked by more numerous and larger fishes than the period from November through May (Fig. 4).

Hydrographic conditions in the Florida Current proved to be remarkably stable throughout the year. Surface temperature varied from a low of 23.5°C in

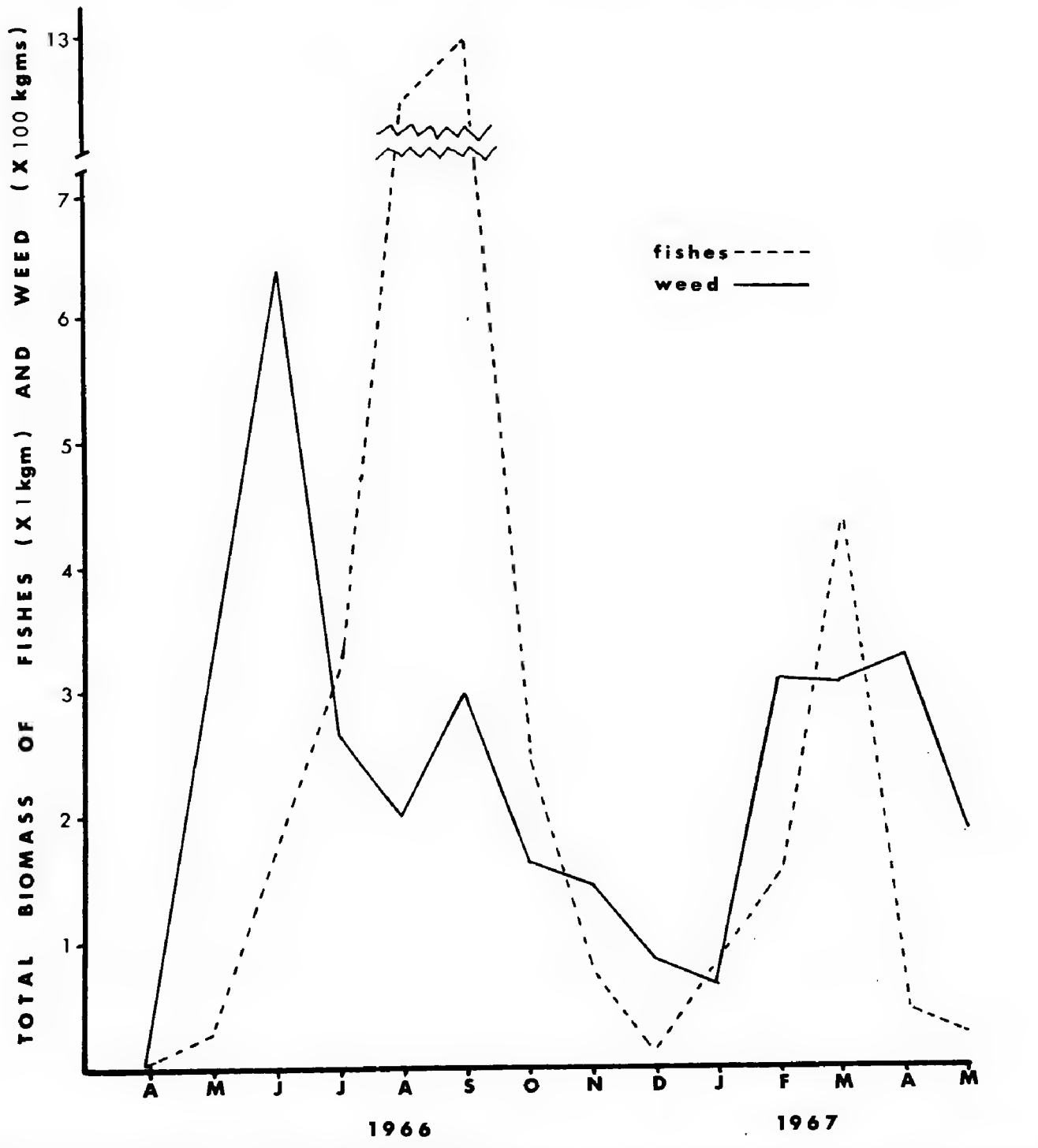

FIG. 3. A comparison of the total biomass of sargassum with the total biomass of associated fishes.

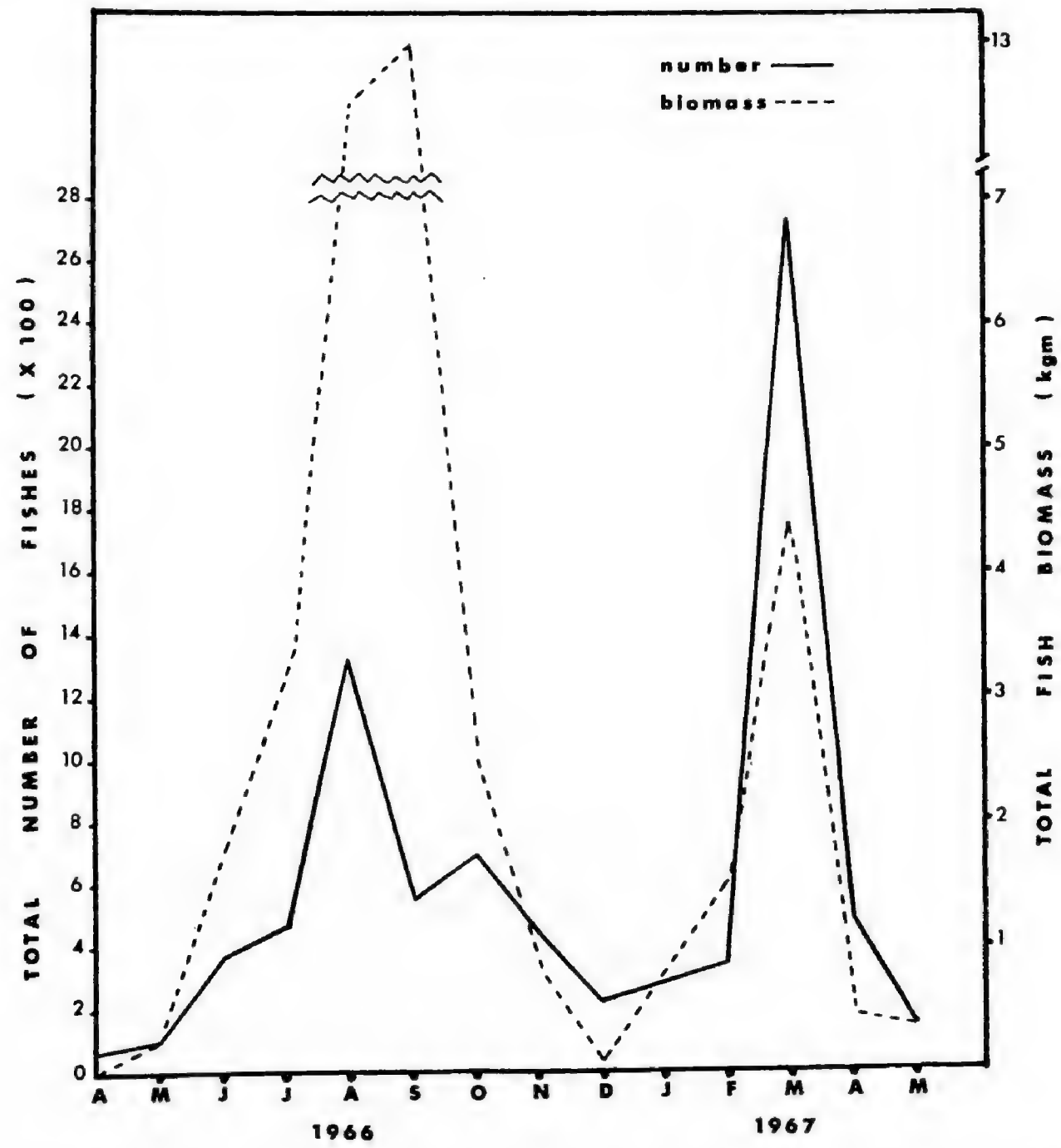

FIG. 4. A comparison of total numbers and total biomass of sargassum associated fishes.

December to a high of 30.1°C in August. Surface salinity ranged from a low of 35.3‰ in May to a high of 37.0‰ in June. There did not appear to be any relationship between numbers of fishes found in sargassum and hydrographic conditions in the Florida Current.

The only night station taken during the study did not reveal a fauna unlike that collected earlier during the day. Likewise, there were no apparent differences between two samples taken slightly inshore of the Florida Current and those taken several hundred meters to the east within the current.

The sargassum fishes have been separated into four categories based on their relative abundance, frequency of occurrence and ecological relationship to the weed. The first group has been designated coincidentally associated fishes based on their rare occurrence, less than 20 specimens. The second group has been defined as moderately associated fishes. These fishes were rare, less than 20 specimens, but based on previous reports they were thought to be associated with sargassum either for a source of food or shelter. Because of the paucity of speci-

mens, fishes belonging to the two previously mentioned groups will only be listed and not discussed (Table 1). The third category has been designated as seasonally occurring sargassum fishes. These fishes were found in relative high numbers, but occurred during less than 6 months of the study (Table 2) and will be discussed briefly. The last and most important catagory has been listed as fishes closely associated with sargassum. These fishes were found in numbers greater than 20 specimens and occurred during 6 months or more of the study.

SEASONALLY OCCURRING FISHES

Hemiramphidae

Hemiramphus balao LeSueur

The balao was present in March through June, and November through February, reaching its peak abundance in the latter period (Table 2). This species is probably a predator on the members of the sargassum community.

Exocoetidae

Cypselurus heterurus (Rafinesque)

Adults of this flyingfish have been reported to use sargassum and other flotsam as a substratum for their eggs, the young use the weed as a refuge (Breder, 1938). Both adults and young of this species were taken under sargassum in May and November through February.

TABLE 1

A list of the coincidental and moderately associated sargassum fishes found in the Florida Current
Coincidental = (C), Moderately associated = (M)

Carcharhinidae		Mullidae	
Cacharhinus falciformis	(C)	*Upeneus parvus*	(C)
Clupeidae		Xiphiidae	
Sardinella anchovia	(C)	*Xiphias gladius*	(C)
Belonidae		Monacanthidae	
Tylosurus acus	(M)	*Alutera monoceros*	(M)
Exocoetidae		*A. schoepfi*	(M)
Parexocoetus brachypterus	(C)	*A. heudelotii*	(M)
Exocoetus obtusirostris	(C)	*Cantherhines macrocerus*	(M)
Hirundichthys affinis	(M)	*Monacanthus tuckeri*	(M)
Centriscidae		Balistidae	
Macrorhamphosus sp.	(C)	*Canthidermis maculatus*	(M)
Syngnathidae		*C. sufflamen*	(M)
Syngnathus louisianae	(C)	*Xanthichthys ringens*	(M)
Carangidae		Tetraodontidae	
Caranx hippos	(M)	*Sphaeroides sp.*	(C)
Decapterus macarellus	(M)	Diodontidae	
D. tabl	(M)	*Diodon holacanthus*	(M)
Elagatis bipinnulatus	(M)	*D. hystrix*	(M)
Seriola fasciata	(M)		
S. zonata	(M)		

TABLE 2

The number, relative abundance, seasonal occurrence, mean size and size ranges of seasonally occurring sargassum fishes found in the Florida Current

Species	March–June Number	March–June Number per hundred kgm of weed	March–June Mean size (mm)	March–June Size range (mm)	July–October Number	July–October Number per hundred kgm of weed	July–October Mean size (mm)	July–October Size range (mm)	November–February Number	November–February Number per hundred kgm of weed	November–February Mean size (mm)	November–February Size range (mm)
Hemiramphidae												
Hemiramphus balao	16	0.89	80	37–98	0	——	—	——	31	5.00	87	47–110
Exocoetidae												
Cypselurus heterurus	3	0.16	27	12–51	0	——	—	——	60	9.70	—	larvae–90
Carangidae												
Trachurus lathami	1,889	105.0	48	12–62	0	——	—	——	0	——	—	——
Scombridae												
Scomber japonicus	240	13.40	57	37–78	0	——	—	——	0	——	—	——
Mugilidae												
Mugil curema	0	——	—	——	0	——	—	——	159	25.80	—	larvae

Carangidae

Trachurus lathami Nichols

The rough scad was collected with *Scomber* and *Decapterus* in very large schools and only in March. Stomach analysis of 14 specimens are shown in Table 3. Much of the material was not identifiable, but sargassum crustaceans and many copepods were evident.

TABLE 3

Stomach analysis of the eight most abundant sargassum fishes. Stomach contents listed in percent of occurrence. Number in parentheses is number of specimens examined. A = *Trachurus lathami*, B = *Caranx crysos*, C = *C. ruber*, D = *Seriola rivoliana*, E = *Stephanolepis hispidus*, F = *S. setifer*, G = *Balistes capriscus*, and H = *Histrio histrio*

Stomach contents	Fish species A (14)	B (42)	C (28)	D (8)	E (75)	F (66)	G (26)	H (77)
Sargassum fragments	..	10	..	75	73	76	31	3
Empty	40	5	4	..	..	..	19	12
Invertebrates								
Unidentified	26	38	4	..	..	..	31	25
Hydroids	..	..	..	..	84	48	15	..
Copepods	26	31	96	..	25	8	31	..
Phylosoma larvae	..	14	..	..	..	..	..	..
Shrimp								
Leander tenuicornis	..	40	7	50	..	11	23	14
Latrudes fucorum	..	..	..	..	4	6	..	19
Zoea, post larvae	..	..	21	..	..	..	..	..
Crabs								
Portunus sayi	..	..	..	..	3	11	8	..
Pycnogonid	..	..	4	..	11	2	4	..
Barnacles	..	..	..	..	32	29	27	..
Tunicates	..	.	..	..	1	23	..	..
Polychaetes	..	..	..	..	12	..	12	..
Bivalvia	..	..	..	..	1	..	..	..
Gastropods	..	..	..	..	..	5	12	..
Platyhelminthes	..	..	..	..	..	3	..	..
Vertebrates								
Fishes								
Unidentified	8	2	4	38	..	..	..	27
Synodus (larvae)	..	5	..	..	..	..	..	..
Coryphaena sp.	..	..	..	13	..	..	..	..
Syngnathus sp.	..	..	..	25	..	..	..	..
Carangid	..	..	.	..	..	..	..	10
Trachurus lathami	..	..	..	..	..	..	..	4
Caranx sp.	..	..	..	25	..	..	..	1
C. crysos	..	..	..	25	..	..	..	..
Scomber japonicus	..	..	..	..	..	..	..	1
Cantherhines pullus	..	..	..	25	..	..	..	1
Balistid	..	..	..	38	..	..	..	..
Canthidermis sp.	..	..	..	25	..	..	..	..
Stephanolepis sp.	..	..	..	..	..	..	..	6
Histrio histrio	..	..	..	..	..	..	..	1
Fish eggs	..	..	..	..	..	2	..	..

Scombridae

Scomber japonicus Houttuyn

The Pacific mackerel was found only during March, always schooling with *Trachurus* and *Decapterus*. *Scomber* probably uses sargassum fauna as a supplemental source of food much like *Trachurus*.

Mugilidae

Mugil curema Valenciennes

Numerous schools of larval silver mullet (8–20 mm) were observed and captured near or among sargassum from December through February. Larval mullet probably use sargassum as a refuge to avoid predation.

FISHES CLOSELY ASSOCIATED WITH SARGASSUM

Syngnathidae

Syngnathus floridae mckayi (Jordan and Gilbert)

Male brood pouches of this pipefish contained eggs from May through December. The smallest mean size and the greatest abundance occurred from July through October (Table 4). *S. floridae mckayi* apparently use sargassum as a shelter. Several specimens were taken among sargassum off the Azores from the USNS Gilliss and will be discussed later.

Syngnathus pelagicus Linnaeus

The sargassum pipefish is endemic to the pelagic sargassum community and was found throughout the year. Males of this species were found with eggs in their brood pouches in November and May. Böhlke and Chaplin (1968) observed eggs in July in the Bahamas.

Lobotidae

Lobotes surinamensis (Bloch)

Young specimens of the triple tail were taken from summer through winter, with a peak in abundance occurring in early fall (Table 4). Young taken from sargassum were discussed by Böhlke and Chaplin (1968), who believed that young *Lobotes* were not established in sargassum. The tendency of *Lobotes* to float on their side at the surface and also the presence of rough scales and sharp opercular spines appears to ideally suit *Lobotes* for life in sargassum (Breder, 1949). A small specimen was found in sargassum off the Tortugas by Longley and Hildebrand (1941). The sargassum weed seems to be an important habitat for the young triple tail, while the more independent adults probably use the faunal complex as an occasional source of food.

Carangidae

The family carangidae is one of the most numerous and diverse groups found among sargassum. According to Böhlke and Chaplin (1968) most, if not all of the carangids are probably pelagic spawners. Many species have apparently adopted the sargassum as a nursery. The very young jacks (below 20 mm) were

TABLE 4

The number, relative abundance, seasonal occurrence, mean size and size ranges of fishes closely associated with sargassum found in the Florida Current

Species	March–June				July–October				November–February			
	Number	Number per hundred kgm of weed	Mean size (mm)	Size range (mm)	Number	Number per hundred kgm of weed	Mean size (mm)	Size range (mm)	Number	Number per hundred kgm of weed	Mean size (mm)	Size range (mm)
Syngnathidae												
Syngnathus floridae mckayi	5	0.28	123	87–145	46	4.90	94	48–166	17	2.80	101	68–163
S. pelagicus	5	0.28	134	110–167	9	0.96	129	88–178	9	1.50	108	98–124
Lobotidae												
Lobotes surinamensis	1	0.06	68	68	27	2.90	159	18–250	2	0.32	149	115–183
Carangidae												
Caranx crysos	135	7.50	41	12–111	330	35.30	70	17–136	4	0.65	49	36–65
C. ruber	170	9.50	37	18–87	137	14.60	40	14–89	3	0.49	33	27–43
C. bartholomaei	49	2.70	29	10–77	61	6.50	23	15–72	39	6.30	26	19–35
Seriola rivoliana	14	0.78	37	12–107	25	2.70	137	21–295	13	2.10	47	26–81
S. dumerili	15	0.84	24	13–108	9	0.96	118	62–245	7	1.10	110	52–164
Selar crumenophthalmus	17	0.95	48	37–76	37	4.00	96	54–145	31	5.00	52	36–92
Decapterus punctatus	159	8.90	50	39–54	4	0.43	56	53–60	119	19.30	59	35–78
Coryphaenidae												
Coryphaena hippurus	8	0.45	96	18–170	0	. . .	. .	. . . .	14	2.30	65	15–158
Kyphosidae												
Kyphosus sectatrix	9	0.50	23	10–69	20	2.10	71	11–132	9	1.50	45	24–72
Pomacentridae												
Abudefduf saxatilis	22	1.20	12	8–25	31	3.30	19	11–39	12	1.90	16	12–25
Stromateidae												
Psenes cyanophrys	124	6.90	30	11–79	8	0.85	54	23–89	12	1.90	33	20–78

Table 4 (Continued)

Species	March–June Number	March–June Number per hundred kgm of weed	March–June Mean size (mm)	March–June Size range (mm)	July–October Number	July–October Number per hundred kgm ofweed	July–October Mean size (mm)	July–October Size range (mm)	November–February Number	November–February Number per hundred kgm of weed	November–February Mean size (mm)	November–February Size range (mm)
Monacanthidae												
Stephanolepis hispidus	132	7.40	24	8–57	1,383	148.0	51	12–74	442	71.6	30	7–83
S. setifer	132	7.40	30	9–69	87	9.30	38	25–68	27	4.40	20	11–38
Alutera scripta	12	0.67	88	46–128	33	3.50	108	46–162	5	0.81	92	43–143
Monacanthus ciliatus	12	0.67	21	14–26	6	0.64	19	18–19	2	0.32	19	19
Cantherhines pullus	26	1.50	44	33–67	17	1.80	57	47–76	2	0.32	54	50–59
Balistidae												
Balistes capriscus	1	0.06	30	30	480	51.3	67	13–132	12	1.90	89	35–175
Antennariidae												
Histrio histrio	844	47.0	16	7–115	218	23.3	17	6–58	238	38.6	15	7–58

found within the protection of the weed, while the larger jacks were found progressively further below and away from the weed.

Caranx crysos (Mitchill)

The peak abundance of the blue runner was in June and July (Fig. 5). Based on the mean sizes and modes, and in agreement with Berry (1959), spawning probably takes place principally in early September. *C. crysos* probably migrates inshore between the sizes of 100 and 140 mm (Table 4). The largest specimen I captured in the sargassum was 136 mm, while Berry (1959) had no record of this species inshore smaller than 100 mm. Stomach analysis of 42 specimens appears in Table 2. Phylosoma larvae and copepods were the dominant food in August, while zoea and copepods were the primary food in July.

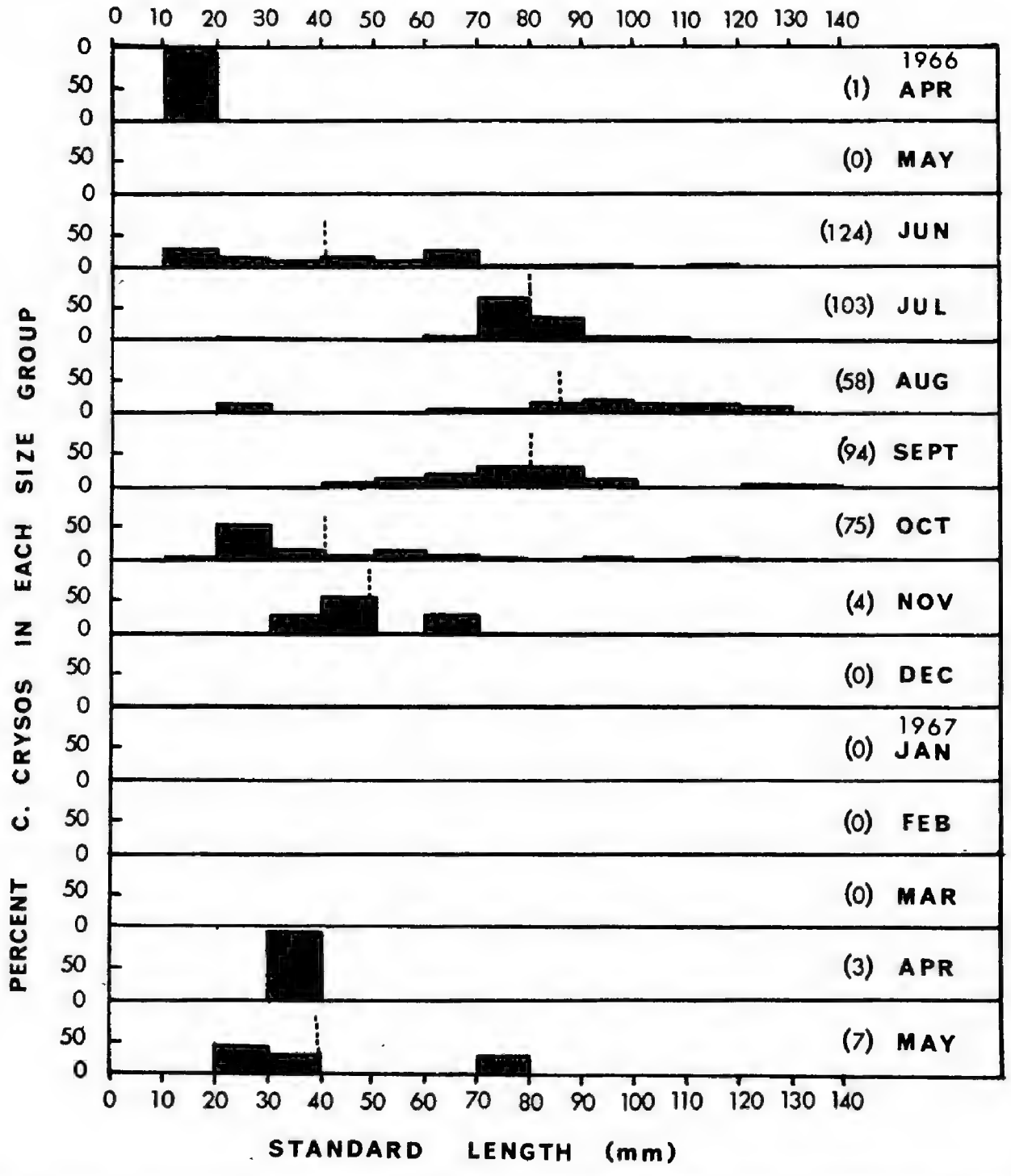

FIG. 5. Size frequency distribution of *Caranx crysos* collected under sargassum in the Florida Current during 1966 and 1967. Dashed lines are mean sizes, numbers in parenthesis are numbers of specimens.

Caranx ruber (Bloch)

The bar jack was found from April through October. Based on size frequency data, spawning probably occurs in July and August (Fig. 6). Based on small specimens, Berry (1959) believed spawning took place from mid February through mid August. He also found *C. ruber* rare inshore north of Jupiter, Florida. Stomach analysis of 28 specimens appears in Table 2. No seasonal differences in feeding were noted.

Caranx bartholomaei Cuvier

Based on small specimens captured the yellow jack probably spawns from February through October; Berry (1959) believed spawning took place from mid February to mid September. Inshore migration of *C. bartholomaei* probably occurs before 75 mm is attained. Berry (1959) found that a 38 mm-specimen

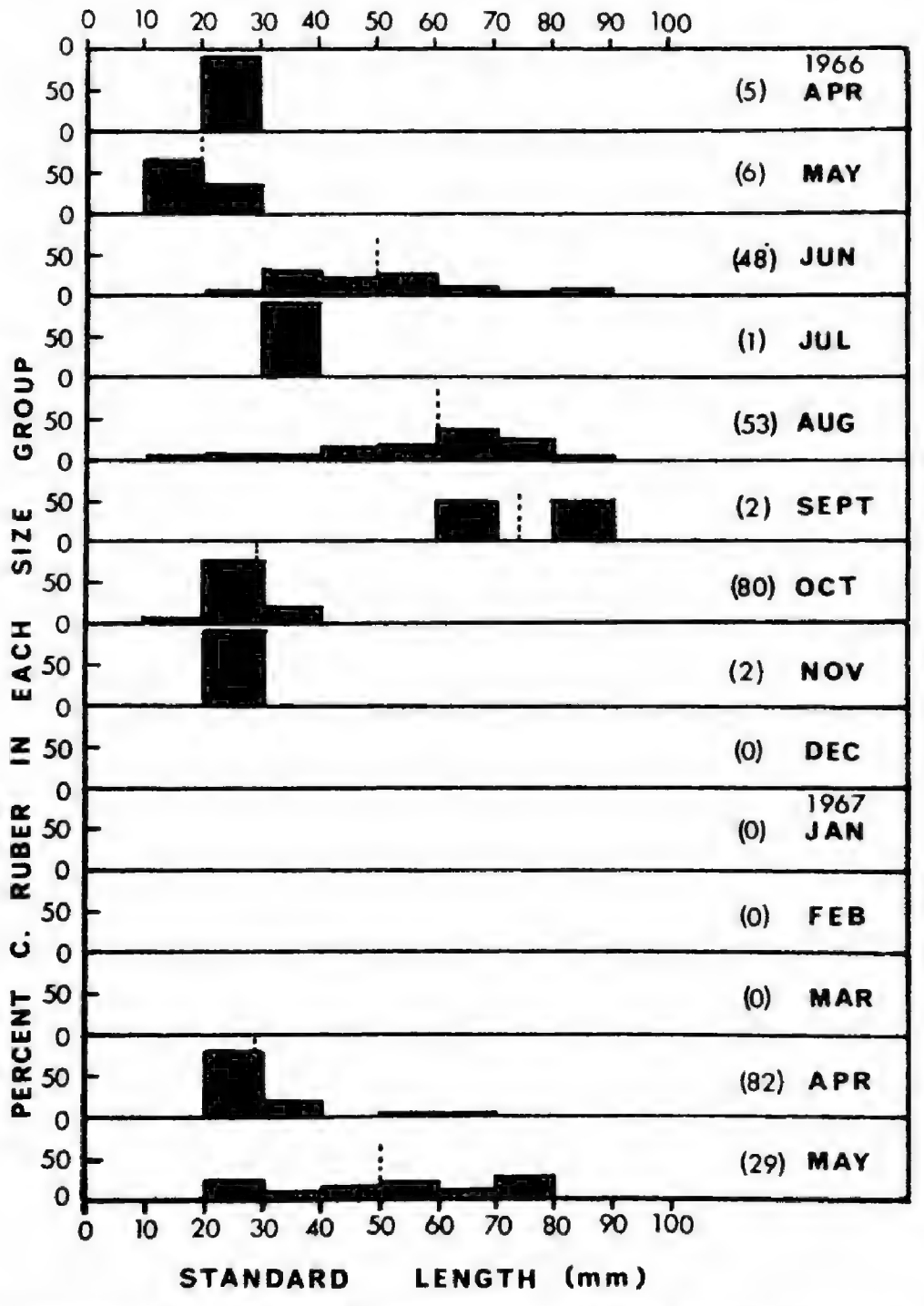

FIG. 6. Size frequency distribution of *Caranx ruber* collected under sargassum in the Florida Current during 1966 and 1967. Dashed lines are mean sizes, numbers in parenthesis are number of specimens.

was the smallest inshore specimen on record. Often onshore winds and currents will drive sargassum and accompanying fishes to inshore areas, particularly at places like south Florida and Cape Hatteras where the Florida Current is close to shore. Roessler (1970) occasionally found small *Caranx*, *Histrio histrio*, and other sargassum associated fishes within the estuary of the Everglades National Park.

Seriola rivoliana Valenciennes and *S. dumerili* (Risso)

Young amberjacks (below 50 mm) appear to use sargassum as a refuge, while larger amberjacks apparently are major predators of the sargassum complex. Stomach analysis of eight specimens of *S. rivoliana* (177–295 mm) can be seen in Table 2. Based on small specimens captured, spawning probably occurs in the spring for both species.

Selar crumenophthalmus (Bloch)

The bigeye scad was found throughout the year with a peak in both abundance and size occurring in summer and fall (Table 4). Stomach analysis of a single 147 mm-specimen of *Selar* revealed carangids, balistids, and sargassum fragments.

Decapterus punctatus (Agassiz)

The round scad was found from November through May with a peak in March. This species probably uses sargassum as a refuge and not as a source of food. Examination of the stomach contents of 10 specimens revealed only copepods. Whether these copepods were residents of the sargassum community or not is not known.

Coryphaena hippurus Linnaeus

The dolphin is one of the most sought after game and food fish and nearly always found in or near sargassum weed. Kojima (1956) believed dolphin take shelter under flotsam (including sargassum) because of a great availability of food. Gibbs and Collette (1959) reported finding filefishes, triggerfishes, jacks, sargassum fragments and sargassum crabs in the stomachs of dolphins. Lewis (1967) found dolphin stomachs contained flyingfishes, filefishes, triggerfishes, puffers and swellfishes.

The present study has yielded an entire ontogenetic series of *C. hippurus*, but curiously not a single specimen of *C. equisetis*; this cannot be explained. Based on the smallest specimens captured, *C. hippurus* may spawn in late November and late March. Based on fecundity studies, Beardsley (1967) believed that peak spawning occurred from January through March, with possible spawning year-around.

Kyphosidae

Kyphosus sectatrix (Linnaeus)

The Bermuda chub was found throughout the year, with the smallest individuals occurring in spring and fall. The young fish appear to be closely associated with sargassum (Moore, 1962), while the adults prefer rocky reef areas

(Böhlke and Chaplin, 1968). It is not known why *K. incisor*, the other species found in the western Atlantic was not found in sargassum.

Pomacentridae

Abudefduf saxatilis (Linnaeus)

Young (below 39 mm) sergeant majors occurred year-around. Perhaps sargassum is a nursery for these littoral fishes. The sergeant major is a circumtropical species, and its young have been found associated with sargassum in other oceans. Besednov (1960) recorded juveniles from sargassum northeast of New Guinea.

Stromateidae

Psenes cyanophrys Culver

The freckled driftfish were most numerous and smallest in the spring (Table 4). According to Böhlke and Chaplin (1968), the adults probably inhabit deeper waters. The young *Psenes* are colored so that they appear well hidden among sargassum.

Monacanthidae

The filefishes, triggerfishes and jacks comprised 74% of all fishes I found in sargassum. The filefishes and triggerfishes make up an important part of the pelagic forage fish fauna as well (Berry and Vogele, 1961). The importance of monacanthids and balistids in the diets of dolphins and tuna have been shown by Gibbs and Collette (1959) and Lewis (1967).

Stephanolepis hispidus (Linnaeus)

The planehead filefish was the most numerous fish found in sargassum (Table 4). *S. hispidus* outnumbered its sibling species *S. setifer* by 5 to 1. *S. hispidus* was in peak abundance in July and August with spawning probably occurring from September through April, based on mean and modal sizes (Fig. 7). Females with immature eggs were observed in December. It is interesting to note that the young of two species of *Stephanolepis* coinhabit the sargassum, while the adults appear to be disjunct; *S. hispidus* a continental species as an adult, and the smaller *S. setifer*, an insular species (F. H. Berry, personal communication). Ida, Hiyama and Kusaka (1967a) have shown that in *S. cirrhifer*, a species found in association with sargassum off Japan, the feeding habits changed with growth. Based on stomach analysis of the young of *S. hispidus* and *S. setifer*, it is evident that their diverse food habits are such that they are compatable, while it is possible that the food habits of the adults make *S. hispidus* and *S. setifer* competitive. Stomach analysis of 75 young *S. hispidus* appears in Table 3. The principal foods from winter through spring were sargassum fragments, hydroids and barnacles; summer foods were sargassum fragments, hydroids and copeopods *Stephanolepis setifer* (Bennett).

The pigmy filefish was most abundant during the summer (Table 4). Based on mean and modal sizes, spawning appears to occur, as with *S. hispidus*, from September through April (Fig. 8). The results of examination of the food habits

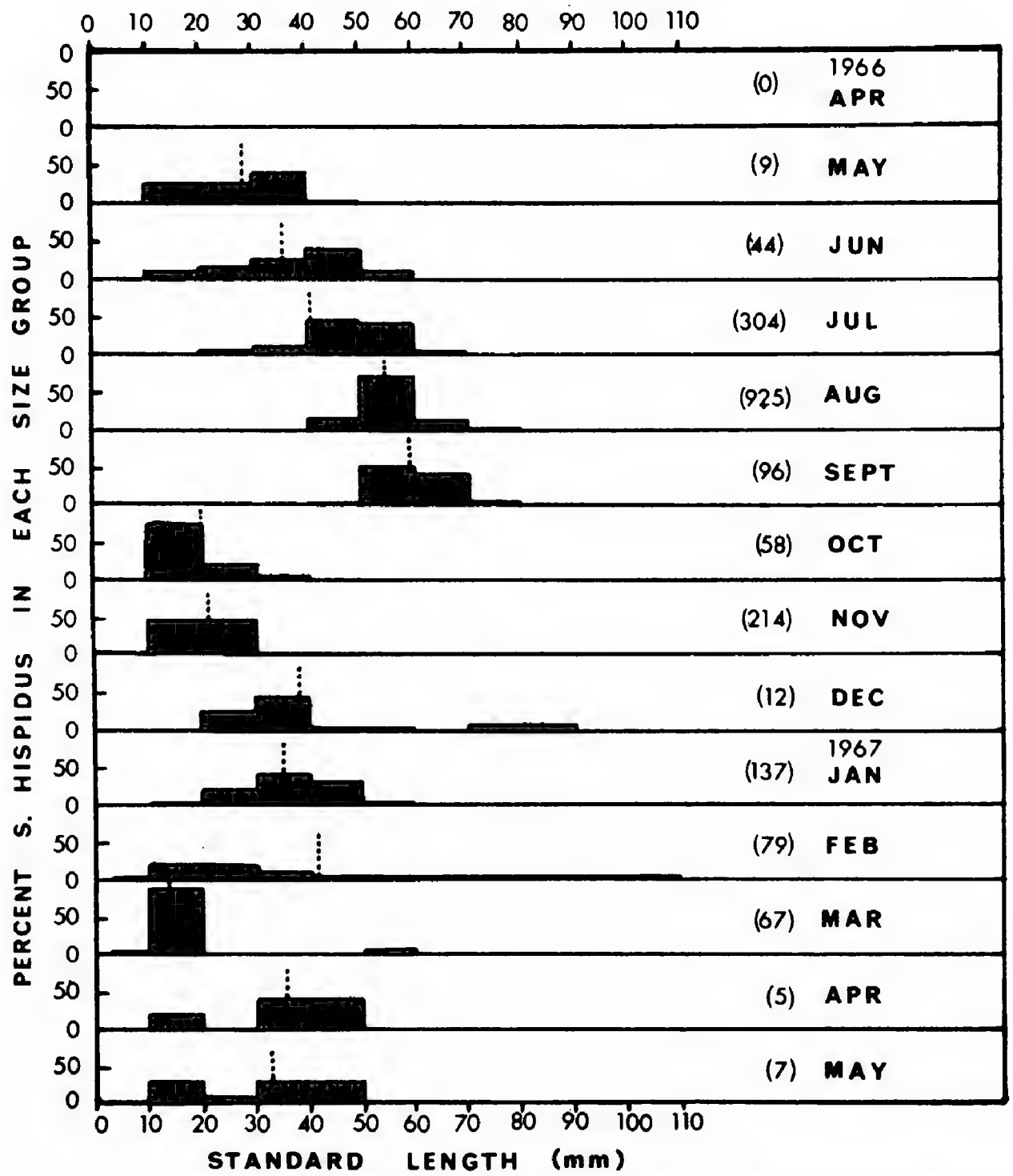

FIG. 7. Size frequency distribution of *Stephanolepis hispidus* collected under sargassum in the Florida Current during 1966 and 1967. Dashed lines are mean sizes, numbers in parenthesis are numbers of specimens.

of 66 young *S. setifer* is shown in Table 3. There was little seasonal variation in feeding other than polychaetes being the dominant food during the summer.

Alutera scripta (Osbeck)

The scrawled filefish was collected throughout the year, with the smallest specimens in August. Young *A. scripta* probably use sargassum as a nursery then migrate inshore at approximately 160 mm.

Monacanthus ciliatus (Mitchell)

The fringed filefish is a common inhabitant of *Thalassia* beds as juveniles and adults. Young specimens (below 27 mm) of *M. ciliatus* were collected in sargassum year-round. Spawning appears to occur year-round because of the nearly constant small mean size and size ranges (Table 4).

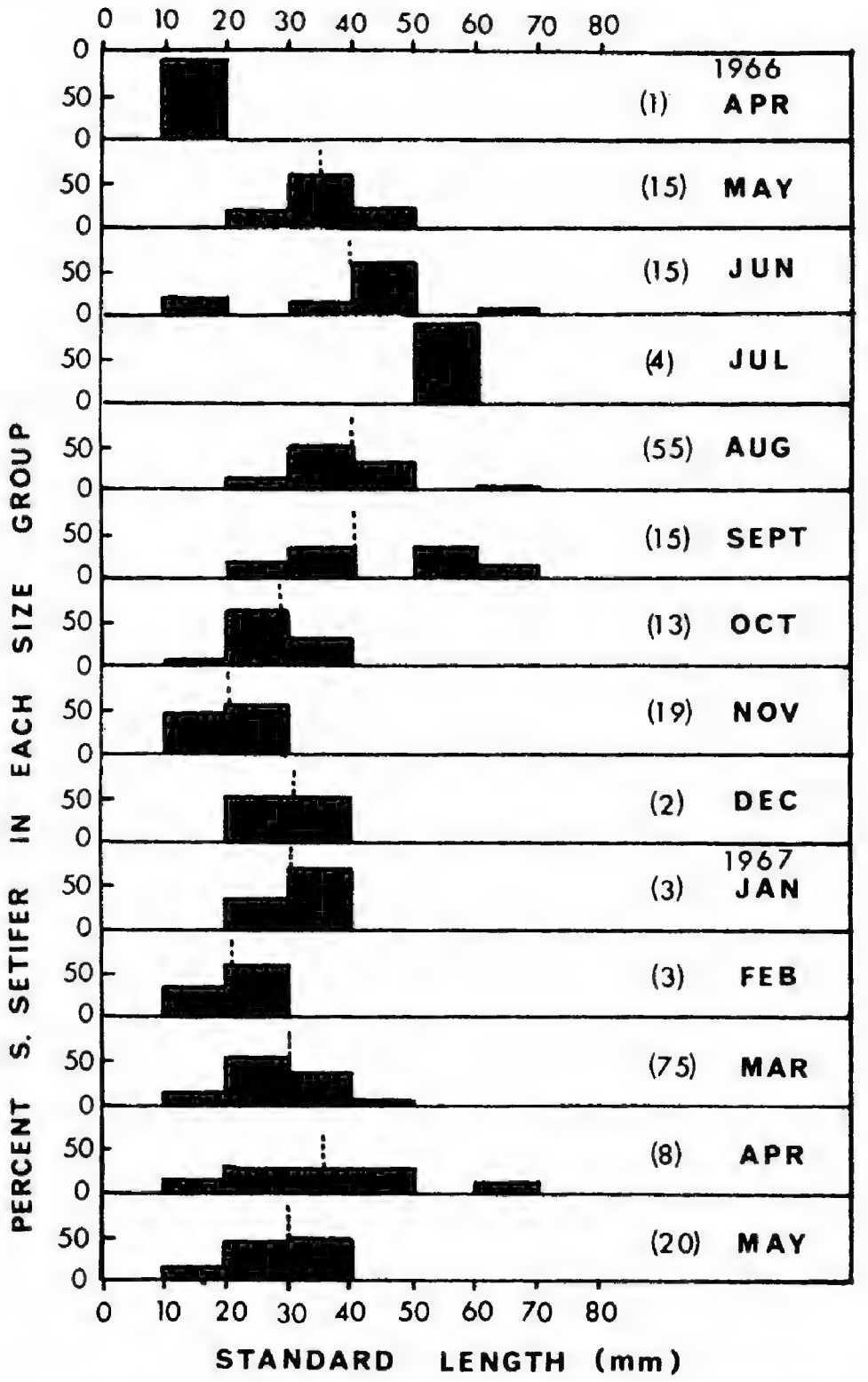

FIG. 8. Size frequency distribution of *Stephanolepis setifer* collected under sargassum in the Florida Current during 1966 and 1967. Dashed lines are mean sizes, numbers in parenthesis are numbers of specimens.

Cantherhines pullus (Ranzani)

The orangespotted filefish is a fairly common sargassum inhabitant along with its rare sibling species *C. macrocerus* (Dooley, 1968). *C. pullus* was in peak abundance in June, and found in low numbers in winter (Table 4). According to Randall (1964), ripe females were found in the Virgin Islands and Puerto Rico from February to June. *C. pullus* apparently spawn in late winter to late spring. The pelagic young inhabit sargassum to approximately 76 mm or less, then migrate to inshore reefs.

Balistidae

Balistes capriscus Gemlin

The gray triggerfish was caught in high numbers from August through October, with very few caught in subsequent months (Fig. 9). Based on the smallest specimens captured, spawning probably occurs from July through October. Stomach analysis of 26 specimens revealed that *B. capriscus* relies heavily on the sargassum complex for food (Table 3).

Antennariidae

Histrio histrio (Linnaeus)

The endemic sargassum fish appeared in 87 of the 102 samples collected in the Florida Current. Length frequency analysis showed an increase in mean size from April through September followed by a sudden influx of 6–15 mm individuals in October (Fig. 10). There was apparently subsequent recruitment of the

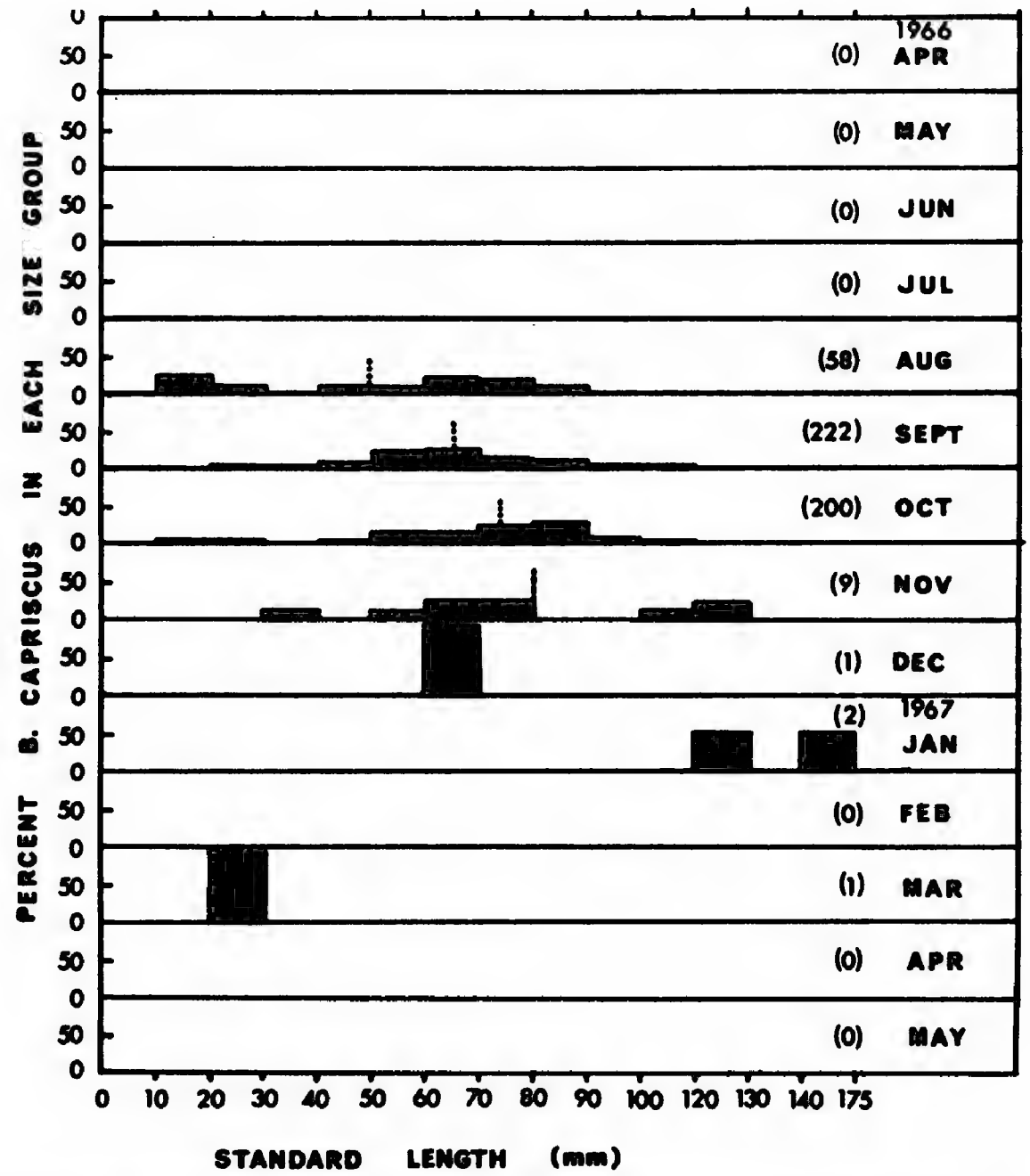

FIG. 9. Size frequency distribution of *Balistes capriscus* collected under sargassum in the Florida Current during 1966 and 1967. Dashed lines are mean sizes, numbers in parentheses are numbers of specimens.

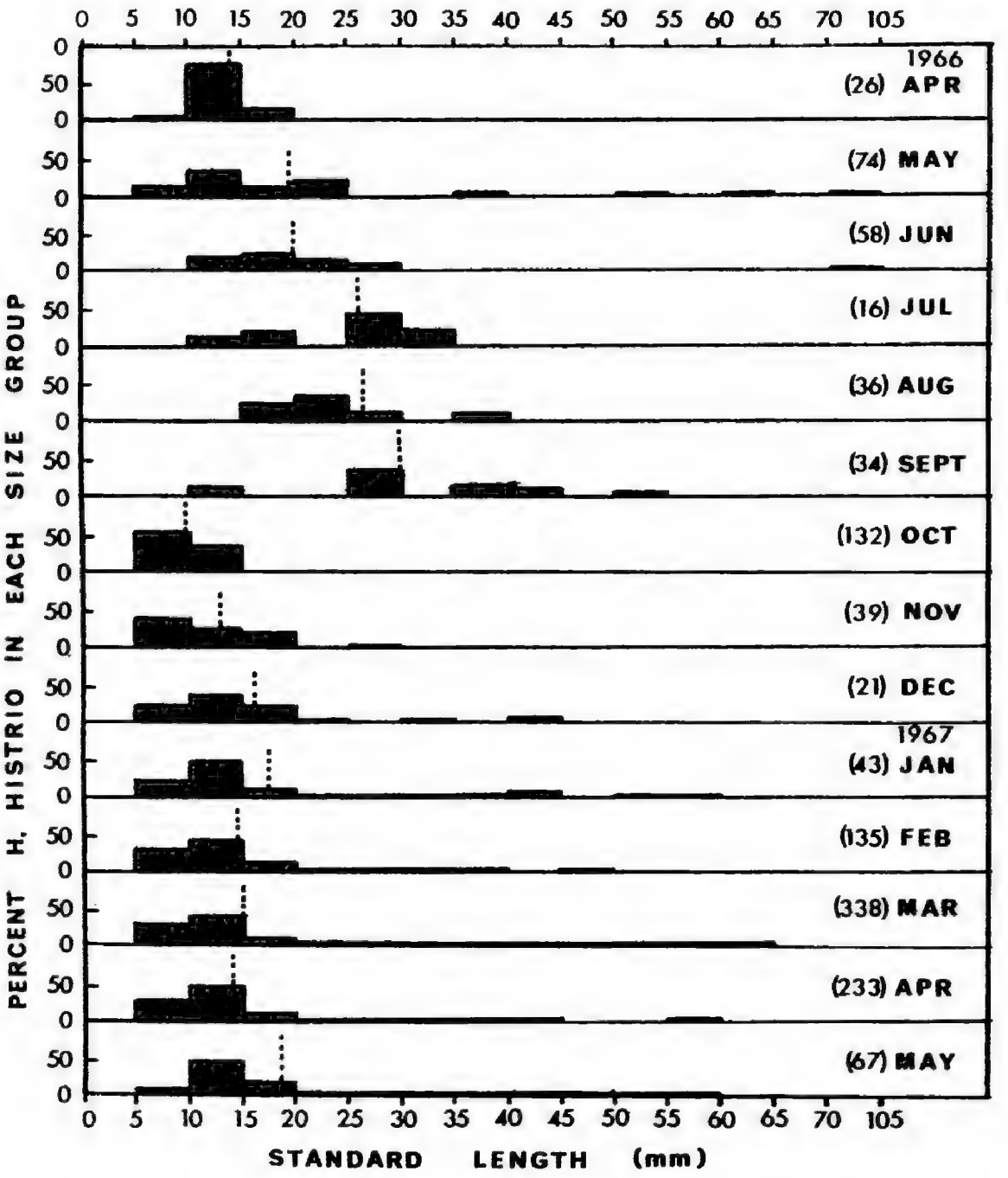

FIG. 10. Size frequency distribution of *Histrio histrio* collected under sargassum in the Florida Current during 1966 and 1967. Dashed lines are mean sizes, numbers in parentheses are numbers of specimens.

smallest size groups (5–10 mm), and emmigration or high mortality of the larger fishes from October through April. Spawning occurred at least from late August through April based on mean and modal sizes (Fig. 10). Adams (1960) suggested that spawning might be year-round. She also found that larval and postlarval *Histrio* (up to 4 mm) occurred at depths from 50 to 600 m. Adams (1960) did not find any *Histrio* larger than 4 mm below a depth of 50 m, and I did not recover any specimen smaller than 6 mm in sargassum. *Histrio* has an enormus mouth and distensible stomach and is a voracious predator within the sargassum community. Adams (1960) found even the larval *Histrio* were carnivorous. It was found in my study that small *Histrio* (below 20 mm) generally fed on sargassum shrimps (carideans), while larger specimens fed mostly on fishes. Stomach analysis of 77 *Histrio* appears in Table 3.

FISH—SARGASSUM RELATIONSHIP

Age of the sargassum community is conjectural because no fossil record for Sargassum is known (C. J. Dawes, personal communication), and only three specimens of a fossil antennariid *Histonotophorus bassani*, a relative of *histrio histrio*, are known from the Upper Eocene (Eastman, 1911). However old the sargassum community, the complex appears to be well established as evidence by its nearly cosmopilitan occurrence in world oceans, the high degree of faunal adaptive coloration, form and behavior (Cott, 1957) and the numerous examples of endemism (10 invertebrates and 2 fishes).

Many hypotheses have been proposed for the causative factors for the fish—sargassum relationships. Prat (1935) suggested the weed offered fishes a source of food, protection from predators, a substratum, a shelter for eggs and larvae, and a mechanical protection from waves. Mitchell and Hunter (1970) demonstrated by laboratory experimentation that fishes associated with drifting kelp were pursued less often, for shorter periods, and captured less frequently by predators. Ida, Hiyama and Kusaka (1967b) clearly showed that most weed associated fishes were dependent upon sargassum for both food and shelter. The present study shows sargassum fishes feed on the sargassum community (Table 3). Damant (1921) believed that fishes were attracted to flotsam because the shade made zooplankton more visible for capture. Senta (1966) found that the kinds of material used in artificial weed experiments seemed to make little difference in the gathering of juvenile fishes. Kojima (1957) found a sargassum filefish reacted positively to shade, while Senta (1966a) found some juvenile fishes were attracted to light. Hunter and Mitchell (1968) discovered fishes seemed to aggregate around three dimentional objects more than two dimentional ones. Factors such as optical fixation (Senta, 1966b; Hunter and Mitchell, 1967), thigmotrophism (Breeder and Nigrelli, 1938), and the use of flotsam as a cleaning station (Gooding and Magnuson, 1967) have been suggested as causing fish to aggregate around floating objects.

It seems probable that sargassum primarily offers protection, as can be seen by adaptive behavior and coloration of the fishes, and a concentration of food in the somewhat barren upper meter of the open sea. Langmuir (1938) first noticed that *Sargassum* aggregated into windows that were oriented along convergencies of sea surface circulatory cells induced by the wind. Sutcliffe, Baylor and Menzel (1963) demonstrated that organo-phosphates concentrate as surface slicks along the convergencies of these "Langmuir Cells." Particulate organics and phosphates from these slicks are broken up and carried by downwelling and would appear to be readily available as a source of nutrients for planktonic organisms (Sutcliffe, Baylor and Menzel, 1963). The high concentrations of plankton found in windows lend support to this hypothesis and would seem to form the basic food source necessary to the sargassum community.

In addition to this allocthonous source of plankton, the sargassum community apparently carries along a resident planktonic population. Yeatman (1962) found six species of littoral copepods clinging to or swimming close to sargassum collected in the North Atlantic. These copepods reproduce while being trans-

ported with sargassum as shown by egg-sacs, numerous nauplii and various immature stages present. Stomach analysis of a 25-mm flyingfish revealed a number of these littoral copepods and led Yeatman (1962) to conclude "*Sargassum* inhibiting copepods furnish food for some fishes as well as for coelenterates, etc. in the Sargasso Sea." Table 3 shows that sargassum jacks, filefishes and triggerfish frequently feed on copepods.

Young jacks live within or close to the protective branches of sargassum and feed heavily on copepods and larval decapod crustaceans. Sub-adult jacks such as *Seriola*, range further from the community and occasionally dart in to feed on shrimp and young fishes that inhabit the weed.

The filefishes and triggerfishes form a second major predatory component of the sargassum community. Filefishes feed manly on hydroids and encrusting bryozoans, injesting large quantities of sargassum leaves in the process; secondarily, filefishes feed on other sargassum invertebrates (Table 3). Triggerfishes depend less on encrusting bryozoans, but otherwise feed similarly to the filefishes.

The third major predator of the sargassum complex is the voracious sargassum fish *Histrio histrio*. *Histrio* is a skillful predator consuming very little superflous weed while selectively feeding on shrimp and young fishes (Table 3).

Fishes that associate with sargassum seem to derive principal benefit from the food and protection offered by the weed. Additional factors such as those discussed probably play a less important role in the gathering of fishes around floating sargassum. Whatever the reasons for the association, it seems probable that these causitive factors would serve to reinforce both innate and acquired aggregation behavior in many of the closely associated fishes. Breder and Halpern (1946) have suggested that such a phenomenon was instrumental in developing schooling behavior in fishes.

ZOOGEOGRAPHIC DISTRIBUTION

Sargassum is transported via major ocean currents and apparently acts as a vehicle for the dispersal of some of its associated organisms. Sargassum—ocean current dispersal is seemingly an active mechanism within the North Atlantic and Pacific Oceans, but probably is very restricted between these systems.

Fell (1967) emphasized the role of ocean currents in the dispersal of marine organisms and theorized that species gradients reflected the direction of successful migration as supported by the distribution of the molluscan genus *Voluta* and other groups. Briggs (1967) disagreed and contended that data from shore fishes suggested that the degree of biological competion was a more important factor in the dispersal of shore animals than the direction of major ocean currents. Briggs further believed that species gradients do not indicate the direction of dispersal, possibly only the success. Scheltema (1966, 1968) has shown impressive evidence for the dispersal of coelenterate, echinoderm, arthropod, annelid and molluscan larvae via ocean currents and its importance to the zoogeography of shallow water tropical species. Yeatman (1962) gave evidence based on plankton samples taken across the North Atlantic, that six species of

littoral harpacticoid copepods probably owe their European and Mediterranean distributions to sargassum association.

Of the fifty-two sargassum fishes identified to species in my study, twenty (38%) are circumtropical, or nearly so; most of these have been recorded from world-wide sargassum communities; eighteen species (35%) have been reported from both sides of the North Atlantic; fourteen species (27%) have been found only in the western North Atlantic. According to drift-bottle data, the minimum time required for surface transport from the Bahamas and Florida to Cape Hatteras, North Carolina (25°–34°N) to the Azores is 145 days (Scheltema, 1966). Sargassum fishes collected off Miami from June through August have been compared to the corresponding species taken from Gulf Stream sargassum off Cape Lookout, North Carolina in July and off the Azores in September (Table 5).

TABLE 5

Comparison of the species composition of sargassum fishes taken from three stations in the North Atlantic. Measurements listed in mm, N = number, $\bar{X}$ = mean size

Species	MIAMI (June–August)			CAPE LOOKOUT, N.C. (July 29–31)			AZORES (September 6)		
	N	$\bar{X}$	Range	N	$\bar{X}$	Range	N	$\bar{X}$	Range
Cypselurus furcatus	..	..	..	6	24	20–33	..	..	..
Syngnathus floridae mckayi	38	97	48–166	..	..	.	2	150	146–154
Caranx crysos	285	64	12–124	30	26	13–55	..	..	..
C. dentex	..	..	..	27	23	14–27	..	..	..
C. latus	..	..	..	2	21	19–23	..	..	..
C. hippos	1	24	24	3	30	29–32	..	..	..
C. ruber	103	55	14–89	6	37	18–50	..	..	..
C. bartholomaei	6	42	16–71	8	17	12–23	..	..	..
Seriola rivoliana	5	81	21–132	6	35	24–56	..	..	..
S. dumerili	8	93	62–121	..	..	..	1	88	88
Trachurus lathami	9	29	15–51	4	17	14–19	..	..	..
Elagatis bipinnulatus	4	63	35–123	1	30	30	..	..	..
Kyphosus sectatrix	5	73	17–108	2	24	18–29	..	..	..
Psenes cyanophrys	23	47	30–79	10	41	12–65	..	..	..
Abudefduf saxatilis	11	20	8–39	2	18	15–20	..	..	..
Pseudopriacanthus altus	..	..	..	8	19	16–22	..	..	..
Coryphaena hippurus	..	..	..	4	30	13–54	1	42	42
Stephanolepis hispidus	1273	52	10–70	194	20	9–50	5	67	54–86
S. setifer	72	38	7–68	1	31	31	..	..	..
Stephanolepis sp.	..	..	..	185	14	10–17	..	..	..
Monacanthus ciliatus	6	18	14–19	2	20	19–20	..	..	..
M. tuckeri	..	..	..	1	16	16	..	..	..
Alutera scripta	34	100	46–162	5	50	34–93	..	..	..
A. heudelotii	1	70	70	1	43	43	..	..	..
Cantherhines pullus	31	48	33–67	5	47	40–53	..	..	..
Canthidermis maculatus	2	59	51–67	1	8	8	..	..	..
C. sufflamen	8	63	12–94	4	39	32–57	..	..	..
Balistes capriscus	58	50	13–99	34	22	11–67	2	77	74–80
Xanthichthys ringens	..	..	..	1	27	27	..	..	..
Diodon holacanthus	..	..	..	2	36	34–37	..	..	..
Histrio histrio	110	22	10–73	2	12	10–14	6	19	10–38

These data from North Carolina and the Azores are based on limited sampling, but probably are indicative of the relative diversity and size composition of sargassum fishes found in these areas. A progressive decrease in the numbers of species can be noted from Miami (54) to Cape Lookout (33) and the Azores (6) (Table 6). Some Caribbean sargassum fishes have ranges that include the Azores, Portugal, Madeira and northern West Africa and can be explained by examination of the North Atlantic surface current pattern. The Florida and Gulf Stream currents carry sargassum associated fishes northward; they are carried eastward to the Azores via the North Atlantic drift, and finally the Canary current carries these expatriates southward to the coasts of Madeira, Portugal and northern West Africa (Fig. 1).

Examples of unsuccessful dispersal are apparent; Fish (1966) reported the occurrence of sargassum and tropical fishes (jacks and filefishes) between Rhode Island and Cape Cod in summer and early fall; Dawson (1962) reported a similar situation in the northern Gulf of Mexico.

Extensive collections by the Japanese show a dimunition of numbers of sargassum fishes as one moves away from the influence of the Kuroshio current. Species numbers decline from a peak of 63 off Sagami Bay and vicinity where the Kuroshio current swins east, to 40 species off Fukuoka in the East China Sea, to a low of 15 species off the Oki Islands in the southern Sea of Japan. Besednov (1960) found 18 species of sargassum fishes off the Fiji Islands far to the south of the principal North Pacific current system.

The North Atlantic and Pacific have analogous but distinct palagic sargassum systems, with approximately 30% of their fishes in common. Both systems show centers of high fish diversity marked by a progressive decrease in numbers of species as one moves away from these areas (Table 6).

The successful dispersal of sargassum associated fishes and invertebrates is undoubtedly brought about by the enhancement of survival offered by sargassum

TABLE 6

Zoogeographic distribution of numbers of species of sargassum associated fishes. The number in brackets is the number of species not represented in area of highest diversity

ATLANTIC	
Miami, Florida (25° 40′ N; 80° 00′ W)	54 species
*Cape Lookout, North Carolina (34° 04′ N; 76° 14′ W)	33 species [4]
†Azores (38° 04′ N; 39° 52′ W)	6 species [0]
Total Atlantic species recorded‡	72 species
§PACIFIC	
Sagami Bay, Japan (35° 00′ N; 139° 00′ E)	63 species
Fukuoka, Japan (33° 50′ N; 130° 30′ E)	40 species [11]
Oki Islands, Japan (36° 00′ N; 133° 00′ E)	15 species [3]
Fiji Islands (20° 00′ S; 170° 00′ E)	18 species [6]
Total Pacific species recorded	77 species

* R/V Eastward cruise E-19-70, July 29–31, 1970.
† USNS Gilliss, cruise 402, 6 September 1967.
‡ Recorded from stations and literature.
§ After (Hirosaki, 1960; Shojima and Ueki, 1964; Ida, Hiyama and Kusaka, 1967a; Uchida and Shojima, 1958; Senta, 1962; Besednov, 1960).

association through food and shelter from predation. Pelagic sargassum in conjunction with major ocean currents appears to be a method whereby some marine organisms have successfully bridged faunal barriers.

ADDENDUM

Since completion of this study the following systematic changes have been made: Monacanthidae was incorporated into Balistidae, Hemiramphidae was placed in Exocoetidae, *Alutera* = (*Aluterus*), *A. heudelotii* = (*heudeloti*), *A. scripta* = (*scriptus*), *Sphaeroides* = *Sphoeroides*, *Diodon holacanthus* = *D.* (*holocanthus*), *Caranx crysos* = *C.* (*fusus*), *Elagatus bipinnulatus* = *E.* (*bipinnulata*). The author of *Psenes cyanophyrs* has been changed from Cuvier to Valenciennes; *Stephanolepis* = (*Monacanthus*).

The following citations should also be included: Hentschel (1922) examined sargassun invertebrates; Germain (1935) summarized much of the early knowledge of the Sargasso Sea; Culliney (1970) found (PO-P) phosphate concentrations two to three times greater in water in floating sargassum than in surrounding water; Carpenter (1970) found the number of species of diatoms attached to pelagic sargassum fewer and also smaller than those found ashore on marine and fresh water plants; Hurka (1971) discussed factors that influenced the gas composition in sargassum vesicles; and Kohlmeyer (1971) described sargassum fungi.

LITTRATURE CITED IN ADDENDUM

CARPENTER, E. J. 1970. Diatoms attached to floating *Sargassum* in the western Sargasso Sea. *Physcologia* **9**(3/4): 269–274.

CULLINEY, J. L. 1970. Measurements of reactive phosphorus associated with pelagic *Sargassum* in the northwest Sargasso Sea. *Limnol. Oceanogr.* **15:** 304–306.

GERMAIN, L. 1935. La mer des Sargasses. *Bull. Inst. oceanogr. Monaco.* **671:** 1–23.

HENTSCHEL, E. 1922. Uber den bewuchs auf den treibenden tangen der Sargassosee. *Mitt. Zool. Jahrb. wiss., Hamburg.* **38:** 1–26.

HURKA, H. 1971. Factors influencing the gas composition in the vesicles of *Sargassum*. *Mar. . .Biol.* **11**(1): 82–89.

KOHLMEYER, J. 1971. Fungi from the Sargasso Sea. *Mar. Biol.* **8**(4): 344–350.

ACKNOWLEDGMENTS

I am deeply grateful to my father James L. Dooley, whose support and efforts made this study possible. Special thanks are due Dr. Martin C. Roessler, University of Miami Rosensteil School of Marine and Atmospheric Sciences, who contributed much effort and advice to this project.

Special thanks are also due Drs. J. C. Briggs, B. C. Cowell and J. L. Simon and to Mr. F. H. Berry for their guidance in this report. The author is grateful to the staff members of N.O.A.A., Tropical Atlantic Biological Laboratory who contributed valuable suggestions and criticisms. The author is indebted to Dr. J. R. Hunter, Tuna Resources Laboratory, N.O.A.A., Dr. F. J. Schwartz, Institute of Marine Sciences, University of North Carolina, and Mr. B. J. Zahuranec, U.S. Naval Oceanographic Office for their assistance.

LITERATURE CITED

ADAMS, J. A. 1960. A contribution to the biology and post-larval development of the sargassum fish, *Histrio histrio* (Linnaeus), with a discussion of the sargassum complex. *Bull. Mar. Sci. Gulf Caribb.* **10**(1): 55–82.

ANDERSON, W. W. 1957. Early development, spawning, growth and occurrence of the silver mullet (*Mugil curema*) along the south Atlantic coast of the United States. *Fishery Bull. Fish Wildl. Serv. U.S.* **57**(119): 396–414.

ARATA, G. F. JR. 1954. A contribution to the life history of the swordfish, *Xiphias gladius* Linnaeuse, from the south coast of the United States and the Gulf of Mexico. *Bull. Mar. Sci. Gulf Caribb.* **4**(3): 184–243.

BEARDSLEY, G. L. JR. 1967. Age, growth, and reproduction of the dolphin, *Coryphaena hippurus*, in the straits of Florida. *Copeia.* **1967** (2): 441–451.

BERRY, F. H. 1959. Young jack crevalles (*Caranx* species) off the southeastern Atlantic coast of the United States. *Fishery Bull. Fish Wildl. Serv. U.S.* **59**(152): 417–535.

————. 1968. A new species of carangid fish (*Decapterus tabl*) from the western Atlantic. *Contr. Mar. Sci. Univ. Tex.* **13**: 145–167.

BERRY, F. H. and L. E. VOGELE. 1961. Filefishes (Monacanthidae) of the western North Atlantic. *Fishery Bull. Fish Wildl. Serv. U.S.* **61**(181): 61–109.

BESEDNOV, L. N. 1960. Some data on the ichthyofauna of Pacific Ocean flotsam. Tr. Inst. Okeanol. Acad. Sci. USSR. **41**: 192–197. (Transl. by W. G. Van Campen, avail. BCF, Biol. Lab., Honolulu, Hawaii).

BÖHLKE, J. E. and C. C. G. CHAPLIN. 1968. *Fishes of the Bahamas and adjacent tropical waters.* Livingston Publ. Co., Wynnewood, Pa. 771 p.

BREDER, C. M. JR. 1938. A contribution to the life histories of Atlantic flying fishes. *Bull. Bingham oceanogr. Coll.* **6**(5): 1–126.

————. 1949. On the behavior of *Lobotes surinamensis. Copeia.* **1949**(4): 237–242.

BREDER, C. M. JR. and R. F. NIGRELLI. 1938. The significance of differential locomotor activity as an index to the mass psychology of fishes. *Zoologica. N.Y.* **23**(1): 1–29.

BREDER, C. M. JR. and F. HALPERN. 1946. Innate and acquired behavior affecting the aggregation of fishes. *Physiol. Zool.* **19**(2): 154–190.

BRIGGS, J. C. 1967. Dispersal of tropical marine shore animals: Coriolis parameters or competition? *Nature, Lond.* **216**(5113): p350.

BRUUN, A. F. 1935. Flyingfishes (*Exocoetidae*) of the Atlantic/systematic and biological studies. *Dana Rep.* **6**: 1–108.

BURKENROAD, M. D. 1939. Hydroids on pelagic sargassum *In:* Pelagic sargassum vegetation of the North Atlantic by A. E. Parr. *Bull. Bingham oceanogr. Coll.* **6**(7): 23–25.

CALDWELL, M. C. 1962. Development and distribution of larval and juvenile fishes of the family Mullidae of the western North Atlantic. *Fishery Bull. Fish Wildl. Serv. U.S.* **62** (213): 403–457.

COLLETTE, B. B. 1962. *Hemiramphus bermudensis*, a new halfbeak from Bermuda, with a survey of endemism in Bermudian shore fishes. *Bull. Mar. Sci. Gulf Caribb.* **12**(3): 432–449.

CONOVER, J. T. and J. McN. SIEBURTH. 1964. Effect of sargassum distribution on its epibiota and antibacterial activity. Botanica Mar. **6**(Fasc. ½): 147–157.

COTT, H. B. 1957. *Adaptive coloration in animals.* Methuen and Co. Ltd., London. 508 p.

DAWSON, C. E. 1962. New records and notes on fishes from the northcentral Gulf of Mexico. *Copeia.* **1962**(2): 442–444.

DEACON, G. E. R. 1942. The Sargasso Sea. *Geogrl. J.* **99**(1): 18–28.

DAMANT, G. C. C. 1921. Illumination of plankton. *Nature*, Lond. **108**: 42–43.

DOOLEY, J. K. 1968. Young filefishes, *Cantherhines macrocerus* and *C. pullus. Copeia.* **1968** (4): 863–867.

EASTMAN, C. R. 1911. Catalog of fossil fishes in the Carnegie Museum. I. Fishes from the Upper Eocene of Monte Bolca. *Mem. Carneg. Mus.* **4**(7): 349–391.

EKMAN, S. -1967. *Zoogeography of the sea.* (reprint) Sidgwick and Jackson, London. 417 p.

FALLER, A. J. and A. H. WOODCOCK. 1964. The spacing of windrows of sargassum in the ocean. J. Mar. Res. **22**(1): 22–29.

FELL, H. B. 1967. Resolution of Coriolis parameters for former epochs. *Nature*, Lond. **214** (5094): 1192–1198.

FINE, M. L. 1970. Faunal variation on pelagic *Sargassum*. *Mar. Biol.* **7**(2): 112–122.

FISH, M. P. 1966. Gulf Stream brings fish visitors to Rhode Island. *Maritimes*. **10**(4): 9–10.

GIBBS, R. H. JR. and B. B. COLLETTE. 1959. On the identification, distribution and biology of the dolphins, *Coryphaena hippurus* and *C. equisetis*. *Bull. Mar. Sci. Gulf Caribb.* **9**(2): 117–152.

GOODING, R. M. and J. J. MAGNUSON. 1967. Ecological significance of a drifting object to pelagic fishes. *Pacif. Sci.* **21**(4): 486–497.

HACKETT, H. E. 1963. A preliminary list of the organisms of of the pelagic sargassum complex. *Mimeo. Duke Univ.*, Durham, North Carolina. 6 p.

HEDGPETH, J. W. 1953. An introduction to the zoogeography of the northwestern Gulf of Mexico with reference to the invertebrate fauna. *Publs. Inst. Mar. Sci. Univ. Texas.* **3**(1): 111–211.

————. 1957. Marine biogeography *In:* Treatise on marine ecology and paleoecology. vol. I. marine ecology (J. W. Hedgpeth ed.). *mem.* **67**, *Geolog. Soc. Amer.* 1296 p.

HERALD, E. S. 1965. Studies on the Atlantic American pipefishes with descriptions of new species. *Proc. Calif. Acad. Sci. Ser. 4* **32**(12): 363–375.

HIROSAKI, Y. 1960. Some ecological observations on fishes in Sagami Bay appearing together with the drifting seaweeds. *J. Fac. Sci. Hokkaido Univ. Ser. 6.* **14**(3): 435–442.

————. 1960a. Observations and experiments on the behavior of fishes toward floating objects in aquarium (prelim. report). *Ibid.* **14**(3): 320–326.

————. 1963. Ecological study on fishes with the drifting sea weeds. I. method of studies and environmental factors (in Japanese). *Misc. Rep. Res. Inst. Nat. Resour., Tokyo.* **60**: 66–75.

————. 1963a. Ecological study on fishes with the drifting sea weeds. II. Records of weeds and fishes (in Japanese). *Ibid.* **61**: 77–84.

————. 1964. Ecological study on fishes with the drifting sea weeds. III. Accompanying animals excluded fishes (in Japanese). *Ibid.* **62**: 63–70.

————. 1965. Ecological study on fishes with the drifting sea weeds. V. Relation between kinds, volume and freshness of weeds and catches of fishes, etc. (in Japanese). *Ibid.* **64**: 20–29.

HUNTER, J. R., D. AASTED and C. T. MITCHELL. 1966. Design and use of a miniature purse seine. *Progve Fish Cult.* **28**(3): 175–179.

HUNTER, J. R. and C. T. MITCHELL. 1967. Association of fishes with flotsam in the offshore waters of Central America. *Fishery Bull. Fish Wildl. Serv. U.S.* **66**(1): 13–29.

————. 1968. Field experiments on the attraction of pelagic fish to floating objects. *J. Cons. perm. int. Explor. Mer.* **31**(3): 427–434.

HYMAN, L. H. 1939. Acoel and polyclad turbellaria from Bermuda and the sargassum. Bull. Bingham oceanogr. Coll. **3**(1): 1–26.

IDA, H., Y. HIYAMA and T. KUSAKA. 1967. Study of fishes gathering around floating seaweed. I. Abundance and species composition. *Bull. Jap. Soc. scient. Fish.* **33**(10): 923–929.

————. 1967a. Study on fishes gathering around floating seaweed. II. Behavior and feeding habit. *Ibid.* **33**(10): 930–936.

IMAMURA, Y., M. INOUE, M. OGURA and S. TAKEUCHI. 1965. Fishing of dolphin, *Coryphaena hippurus*, by bamboo raft in the southwest coast of Japan Sea (in Japanese). *J. Tokyo Univ. Fish* **51**(1): 81–86.

KOJIMA, S. 1955. A study of dorado fishing conditions in the western part of the Japan Sea. *Bull. Jap. Soc. scient. Fish.* **20**(12): 1044–1049. (Transl. available, BCF., Honolulu, Hawaii.)

————————. 1956. Fishing for dolphins in the western part of the Japan Sea. II. Why do fish take shelter under floating materials? *Ibid.* **21**(10): 1049–1052. (Transl. available, BCF., Honolulu, Hawaii.)

————————. 1957. Reactions of fish to a shade of floating substances. (In Japanese, English summary.) *Ibid.* **22**(12): 730–735.

————————. 1960. Fishing for dolphins in the western part of the Japan Sea. V. Species of fish attracted to bamboo rafts. *Ibid.* **26**(4): 379–388. (Transl. available, BCF., Honolulu, Hawaii.)

————————. 1960a. Fishing for dolphins in the western part of the Japan Sea. VI. Behavior of fish gathering around bamboo rafts. *Ibid.* **26**(4): 383–388. (Transl. available, BCF., Honolulu, Hawaii.)

————————. 1961. Studies on fishing conditions of the dolphin, *Coryphaena hippurus*, in the western region of the Sea of Japan. III. On food contents of the dolphin. *Ibid.* **27**(7): 625–629. (Transl. available, BCF., Honolulu, Hawaii.)

————————. 1966. Studies on fishing conditions of the dolphin, *Coryphaena hippurus*, in the western regions of the Sea of Japan. XI. School of dolphins accompanying various kinds of flotages. (In Japanese, English summary.) *Ibid.* **32**(8): 647–651.

KRÜMMEL, O. 1891. Die nordatlantische Sargassosee. *Petermanns Mitt.* **37**(Taf. 10): 129–141.

KUNTZE, O. 1881. Revision von *Sargassum* und das sogenannte Sargasso Meer. A. Engler. *Bot. Jb.* **1**.

LANGMUIR, I. 1938. Surface motion of water induced by wind. *Science, N.Y.* **87**(2250): 119–123.

LEGASPI, V. A. 1956. A contribution to the life history of the nomeid fish *Psenes cyanophyrs* Cuvier and Valenciennes. *Bull. mar. Sci. Gulf Caribb.* **6**(3): 179–199.

LEWIS, J. B. 1967. Food of the dolphin, *Coryphaena hippurus* Linnaeus, and of the yellowfin tuna, *Thunnus albacares* (Lowe), from Barbabos, West Indies. *J. Fish. Res. Bd. Can.* **24**(3): 683–686.

LONGLEY, W. H. and S. F. HILDEBRAND. 1941. Systematic catalogue of the fishes of Tortugas, Florida. *Pap. Tortugas Lab.*, **34** (Carnegie Inst. Washington Publ. 535): 331 p.

MARKKAVEEVA, E. G. 1965. The biocenosis of sargasso algae in the Red Sea (In Russian). *In: Bentos, Kiev: Dumka Nauk.* 81–93.

MATHER, F. J. III. 1958. A preliminary review of the amberjacks, genus *Seriola*, of the western Atlantic. *In: Proc. Intern. Game Fish Confer.*, mimeogr. rpt. Miami Beach, Florida 19 Nov. 1958: 1–13.

MATSUI, T. 1967. Review of the mackeral genera *Scomber* and *Rastrelliger* with a description of a new species of *Rastrelliger*. *Copeia.* **1967**(1): 71–83.

McKENNEY, T. W. 1961. Larval and adult stages of the stromateoid fish *Psenes regulus*, with comments on its classification. *Bull. mar. Sci. Gulf Caribb.* **11**(2): 210–236.

McKENNEY, T. W., E. C. ALEXANDER and G. L. VOSS. 1958. Early development and larval distribution of the carangid fish, *Caranx crysos* (Mitchell). *Bull. mar. Sci. Gulf Caribb.* **8**(2): 167–200.

MITCHELL, C. T. and J. R. HUNTER. 1970. Fishes associated with drifting kelp, *Macrocystis pyrifera*, off the coast of southern California and northern Baja California. *Calif. Fish Game.* **56**(4): 288–297.

MOORE, D. 1962. Development, distribution, and comparison of rudder fishes *Kyphosus sectatrix* (Linnaeus) and *K. incisor* (Cuvier) in the western North Atlantic. *Fishery Bull. Fish Wildl. Serv. U.S.* **61**(196): 451–480.

————. 1967. Triggerfishes (Balistidae) of the western Atlantic. *Bull. mar. Sci.* **17**(3): 689–722.

MUKAI, H. 1971. The phytal animals on the thalli of *Sargassum serratifolium* in the *Sargassum* region, with reference to their seasonal fluctuations. *Mar. Biol.* **8**(2): 170–182.

NICHOLS, J. T. 1937. Young *Caranx* in the western North Atlantic. *Bull. Bingham oceanogr. Coll.* **7**(2): 1–8.

PRAT. H. 1935. Remarques sur la faune et la flore associées aux sargasses flottantes. Le Naturaliste canadier. **62**: 120–129.

PARR, A. E. 1939. Quantitative observations on the pelagic sargassum vegetation of the western North Atlantic. *Bull Bingham oceanogr. Coll.* **6**(7): 1–94.

RANDALL, J. E. 1964. A revision of the filefish genera *Amanses* and *Cantherhines*. *Copeia.* 1964 (2): 331–361.

ROESSLER, M. A. 1970. Checklist of fishes in Buttonwood Canal, Everglades National Park, Florida, and observations on the seasonal occurrence and life histories of selected species. *Bull. mar. Sci.* **20**(4): 860–893.

SCHELTEMA, R. S. 1966. Evidence for trans-Atlantic transport of gastropod larvae belonging to the genus *Cymatium*. *Deep Sea Res.* **13**: 83–95.

————. 1968. Dispersal of larvae by equatorial ocean currents and its importance to the zoogeography of shoalwater tropical species. *Nature, Lond.* **217**(5134): 1159–1162.

SCHOENER, A. and G. T. ROWE. 1970. Pelagic *Sargassum* and its presence among the deep-sea benthos. *Deep Sea Res.* **17**: 923–925:

SENTA, T. 1962. Studies on floating sea-weeds in early summer around Oki Islands and larvae and juvenile of fishes accompanying them. *Seiro-Seitai* (*Physiol. Ecol.*). **10**(2): 68–78. (In Japanese.)

————. 1965. The importance of drifting seaweeds in the ecology of fishes. (In Japanese.) *Jap. Fish. Resour. Conserv. Agency, Tokyo Fish. Res. Bull.* **13**: 56 p.

————. 1966. Experimental studies on the significance of drifting seaweeds for juvenile fishes. I. Experiments with artificial drifting seaweeds. *Bull. Jap. Soc. scient. Fish.* **32**(8): 639–641.

————. 1966a. Experimental studies on the significance of drifting seaweeds for juvenile fishes. II. Experiments on the effect of light intensity. *Ibid.* **32**(8): 642–646.

————. 1966b. Experimental studies on the significance of drifting seaweeds for juvenile fishes. III. Experiments on visual stimulations. *Ibid.* **32**(9): 693–696.

SHOJIMA, Y. and K. UEKI. 1964. Studies on the larvae and juvenile fishes accompanying floating algae. II. Research in the vicinity of Tsuyazaki, during April, 1958–March, 1959. *Ibid.* **30**(3): 248–254.

SIEBURTH, J. N. and J. T. CONOVER. 1965. *Sargassum* tannin, an antibiotic which retards fouling. *Nature, Lond.* **208**(5005): 52–53.

SUTCLIFFE, W. H. JR., E. R. BAYLOR and D. W. MENZEL. 1963. Sea surface chemistry and Langmuir circulation. *Deep Sea Res.* **10**: 233–243.

TANING, A. V. 1961. On the breeding areas of the swordfish (*Xiphias*) *In:* Papers in mar. Biol. Oceanogr., suppl. vol. **3** *Deep Sea Res.*: 438–450.

TIMMERMANN, G. 1932. Biogeographische untersuchungen über die lebensgemeinschaft des treibenden golfkrautes. *Z. Morph Ökol. Tiere* **25**: 288–335.

UCHIDA, K. and Y. SHOJIMA. 1958. Studies of drifting seaweeds: Larval and juvenile fishes accompanying drifting seaweeds. I. Investigations in the vicinity of Tsuyazaki in fiscal year 1957. *Bull. Jap. Soc. scient. Fish.* **24**(6 and 7): 411–415. (Transl. available, BCF., Honolulu, Hawaii.)

WEIS, J. S. 1968. Fauna associated with pelagic sargassum in the Gulf Stream. *Am. Midl. Nat.* **80**(2): 554–558.

WINGE, O. 1923 The Sargasso Sea, its boundaries and vegetation. *Rep. Dan. oceanogr. Exped.* **3**(2): 1–34.

WOODCOCK, A. H. 1950. Subsurface pelagic sargassum. *J. mar. Res.* **9**(2): 77–92.

YABE, H. and T. MORI. 1950. An observation on the habit of the bonito,*Katsuwonus vagans* and yellowfin, *Neothunnus macropterus*, school under the drifting timber on the surface of the ocean. *Bull. Jap. Soc. scient. Fish.* **16**(2): 35–39. (Transl. available, BSF., Honolulu, Hawaii.)

YEATMAN, H. C. 1962. The problem of dispersal of marine littoral copepods in the Atlantic Ocean, including some redescriptions of species. *Crustaceana* **4**: 253–272.

DEVELOPMENTAL OSTEOLOGY OF THE LINED SOLE, *ACHIRUS LINEATUS* (PISCES: SOLEIDAE)

Charles R. Futch[1], Robert W. Topp[1], and Edward D. Houde[2]

ABSTRACT

Developmental osteology of the lined sole, *Achirus lineatus*, based on a study of 17 specimens, is described and figured. Chronology of osteological development is documented. Study material, ranging from 2.14 to 93.0 mm SL, included cleared and stained specimens, and disarticulated skeletons.

The adult skull is markedly asymmetrical in the olfactory, orbital, and oromandibular regions, with fusion of ethmoid, lateral ethmoid, and prefrontal components. Although mandibular dentition is restricted to left maxillary and dentary, adult asymmetry is less pronounced in the branchiocranium, as well as the posterior elements of the neurocranium. Branchial arches are typically perciform in composition and arrangement. Otoliths are unsculptured, with no annuli apparent.

Paired neural elements of the atlas are autogenous and do not meet dorsomesially. The second neural spine joins the supraoccipital. Parapophyses first join ventromesially on the fifth trunk vertebra. The three posterior vertebrae are involved in caudal fin support. The hemal spine of the penultimate vertebra is autogenous. The two anteriormost dorsal fin rays are supported by a single pterygiophore. The first five pterygiophores are accommodated by notches in the supraoccipital crest. A right pectoral fin is present, having four to six small rays without bony connection to the cleithrum. A single five-rayed pelvic fin is supported by paired basipterygia.

A. lineatus closely resembles the eastern Atlantic genus *Solea* in most details of its neurocranium, trunk vertebrae and caudal skeleton. *Achirus* differs by absence of a lacrymal, greater symmetry of jaw elements, smaller number of caudal vertebrae, and lack of strong lateral apophyses.

In a series of alizarin-stained larval stages, a cumulative sequence of osteological events is documented: 2.14 mm SL—syncranial elements, neural spines, and cleithral elements present, including large postcleithrum; 2.52 mm SL—appearance of autosphenotic, full branchiostegal complement, distinct arcualia, parapophyses, hemal spines, primordial caudal skeleton, and anterior dorsal lepidotrichs; 3.20 mm SL—proliberation of vertical fin rays; 3.57 mm SL—appearance of bones of olfactory region, full vertebral complement, remaining caudal eleemnts, pelvic girdle and fin, and disappearance of postcleithra; 12 to 14 mm SL—all bony elements present, and in approximate adult configuration.

[1] Florida Department of Natural Resources Marine Research Laboratory, St. Petersburg, Florida 33731. Contribution No. 178.

[2] National Marine Fisheries Service, Tropical Atlantic Biological Laboratory, Miami, Florida 33149. Contribution No. 193. Present address: Rosenstiel School of Marine and Atmospheric Sciences, Miami, Florida 33149.

Contributions in Marine Science, Vol. 16, 1972.

INTRODUCTION

Most osteological studies on the Pleuronectiformes have dealt with syncranial asymmetry, (e.g., Kyle, 1921; Gregory, 1933; and Chabanaud, 1936). Norman (1934) and Berg (1940) offered general comments on osteology, Ford (1937) discussed the axial skeleton of selected taxa, and Yazdani (1969) compared jaw morphology and function. A brief description and comparison of osteological features of the young of three species of *Paralichthys* (Bothidae) by Woolcott et al. (1968) is the only known descriptive work on the complete flatfish skeleton.

The following description of developmental and adult osteology of *Achirus lineatus* (Linnaeus) was done in conjunction with a study by Houde et al. (1970), who described development of larval stages of *A. lineatus*, and compared morphology of larvae and juveniles from Tampa Bay, Florida, with a series reared in the laboratory.

ACKNOWLEDGMENTS

Dr. Ronald C. Baird, University of South Florida, and Mr. David Frame, University of Massachusetts, generously provided critical review of the manuscript. We are particularly indebted to Mr. Robert M. Ingle, Chief, Bureau of Marine Science and Technology, Florida Department of Natural Resources, for his continuing encouragement and advice in bringing this study to completion.

MATERIALS AND METHODS

Basic nomenclatural synonymy ofthe skeleton follows Topp and Cole (1968). Articulatory processes of jaw elements follow Yazdani (1969); caudal fin elements follow Monod (1968) and Gosline (1961). Museum prefixes are FSBC (Florida Department of Natural Resources Marine Research Laboratory) and TABL (Tropical Atlantic Biological Laboratory).

Osteology of the adult *Achirus lineatus* was described from three intact cleared and stained skeletons, FSBC 5967, 10.3 mm SL, FSBC 5968, 76.5 mm SL, and FSBC 5969, 14.0 mm SL, from Tampa Bay. Three complete skeletons, FSBC 5969, 10.2 mm SL, Tampa Bay, and FSBC 4362, 92.0 mm SL and 93.0 mm SL, Ponce de Leon Inlet, Volusia County, Florida, were stained with alizarin and disarticulated following the modification of Ossian (1970). Developmental osteology was described from laboratory reared and Tampa Bay larvae. Laboratory material included specimens numbered 26, 3.73 mm SL; 40, 3.31 mm SL; and 42, 5.11 mm SL (uncatalogued. TABL). Tampa Bay material included FSBC 5850L, 3.20 mm SL; FSBC 5868L, 2.14 mm SL; FSBC 5860L, 3.57 mm SL; FSBC 5880L, 2.52 mm SL; FSBC 5883L, 3.35 mm SL; FSBC 5914L, 3.30 mm SL; FSBC 5920L, 3.40 mm SL; and FSBC 5967L, 8.0 mm SL. All skeletons were cleared and stained by the methods of Hollister (1934) and Taylor (1967).

DESCRIPTION

NEUROCRANIUM

Olfactory Region: (Figs. 1A, 1B, 1C, 1D, 2, and 11)

The olfactory region of adult *A. lineatus* is characterized by marked asymmetry and fusion of prefrontal and ethmoid components, forming the right prefrontal complex (rpfc). The right lateral ethmoid (rle) is a small hourglass-shaped bone forming the dorsal, right, and ventral walls of the right olfactory foramen (rof). Ventrally, its base covers part of the prevomer-parasphenoid

suture. A small ventrolateral shelf provides a point of articulation for the right autopalatine. Dorsally, a wide trapezoidal roof fits into a depression in the right prefrontal complex. The latter forms the lateral and anterior walls of the orbit and forms a rostral projection. A boot-shaped element, inseparably fused to the right prefrontal complex, is directed ventrad to the parasphenoid. Its cancellous structure and relative position identify it as the ethmoid component.

The small, tubular autogenous nasals (n), osseous extensions of the supraorbital laterosensory canal, are imbedded in the snout musculature.

The left prefrontal, left lateral ethmoid, and the ethmoid contribute to the left prefrontal complex (lpfc). The left olfactory foramen (lof) is bounded by ethmoid and left lateral ethmoid components. A large cylindrical shaft of the prefrontal component joins ventrally with the lateral ethmoid component, forming a median foramen. Posteriorly, the left prefrontal complex is joined by suture to an extension of the left frontal. Laterally, the ventral face of the left prefrontal articulates with the left autopalatine. The base of the left prefrontal is a long triangular element fitting into a deep depression of the parasphenoid.

The median, edentulous prevomer (pv) has a triangular base fitting into a groove in the parasphenoid. Dorsally, it is flexed toward the right side, and posteriorly, it joins the left and right prefrontal complexes.

Bones of the olfactory region do not appear until metamorphosis begins. All elements except nasals are present in specimens about 3.3 to 3.5 mm SL (Fig. 10), when the left eye has begun migration. Prefrontal complexes and right lateral ethmoid first appear midway between the frontals and parasphenoid. They join to the frontals, then grow ventrad toward the parasphenoid and prevomer. The right nasal appears in larvae at about 5 mm SL, the left shortly thereafter.

Orbital Region (Figs. 1A, 1B, 2, and 11)

Skull asymmetry is pronounced in this region. The right (lower) eye is not enclosed in a bony orbit, but is held in place by muscles, and partially supported by the underlying palatoquadrate arch. The left (upper) eye rests in a large composite ring of bone, the orbit. The orbit is atypical in lacking the bony ring of suborbital bones characteristic of most teleosts.

Anteriorly, the broad lateral edge of the left frontal (lf) joins the left prefrontal complex to comprise the left wall of the orbit. Both left and right prefrontals (lf and rf) contribute to the remainder of the poseterior orbital walls. The right prefrontal complex completes the right wall of the orbit.

The frontals are almost completely separated dorsally by the supraoccipital. The left frontal contributes a mid-dorsal ridge contiguous with the supraoccipital crest.

Each frontal bears a dorsolateral ridge continuous with the corresponding parietal ridges. On each frontal, a strongly ossified housing for the laterosensory canal ends in an anterodorsally extended tubule.

The asymmetric pterosphenoids (pts), arising from two centers of ossification, extend from the frontals to the parasphenoid. A triangular projection descends from each frontal from the posterior aspect of the orbit. These curve to mesial symphysis, and extend ventrad to meet ascending trapezoidal members from the

parasphenoid. Dorsal and ventral elements are bordered posteriorly by the autosphenotics. The left dorsal element sends a small process dorsad to contact an anteroventral alar process of the autosphenotic. No such connection exists on the right side, although there are vestigial processes on the pterosphenoid and autosphenotic.

In 2.14 mm SL larvae, the frontal is the most conspicuous orbital bone. It dominates the neurocranium, forming a dorsal hump. Each has an "eyebrow" shaped spinous epidermal ridge, later to become bony coverings for the laterosensory canal system. At about 2 mm SL (Fig. 7), before eye migration, the frontals become asymmetric. The anterior portion of the right frontal epidermal ridge lengthens and becomes the interorbital "bony ridge" (Jordan and Evermann, 1898). This asymmetry was ascertained by comparison of measurements of the bony ridges and counts of associated spines of both frontals. At metamorphosis (Fig. 9) both frontals are displaced to the right side. The right epidermal ridge is much longer than its left counterpart. Formation of the orbit by suture of frontals with prefrontal complexes was complete in a specimen 8 mm SL.

Dorsal components of the pterosphenoids appear midway between the parasphenoid and the posterior aspect of the orbit in larvae between 6 and 8 mm SL. Union of dorsal and ventral components with the frontals and parasphenoid was complete in a 14 mm specimen.

Otic and Basicranial Region: (Figs. 1A, 1B, 1D, 2, 11)

The asymmetric autosphenotics (aso) are ovate bones poterior to the pterosphenoids. Each sends a process ventrad. In typical teleosts, this process supports the dermosphenotic, the dorsalmost of the suborbital ossicles. Dorsoposteriorly, the dorsalmost of the suborbital ossicles. Dorsoposteriorly, the autosphenotic joins the autopterotic, and posteroventrally it joins the prootic, with which it shares the hemispherical anterior hyomandibular fossa.

The autopterotic (pto) are roughly hatchet shaped with the "handle" pointed anterodorsad. Posteriorly, they join with each prootic just below the deep posterior hyomandibular fossa.

The prootics (pro) are the largest bones of the otic series. They are pierced by anteriorly directed carotid foramina along their junction with the parasphenoid. Anterdorsally, the prootic forms half of the anterior hyomandibular fossa at its junction with the autosphenotic. The left prootic sends an anterior strut mediad to brace the pterosphenoid. A small projection is present on the right prootic but does not touch the pterosphenoid. The prootic contains the trigeminofacialis chamber, as discussed by Goodrich (1958). Although location of nerves and blood vessels was not examined in detail, the trigeminofacialis chamber of *A. lineatus* presumably conforms in structure to that of most perciform fish, as described and figured by Patterson (1964).

The posterior portion of each prootic contributes to encapsulation of the otoliths. Each otolith is oval, the margin unsculptured by rostrum or antirostrum. The surface contacting the concave inner surface of the prootic and basioccipital is convex, the inner surface is flat. Sulci are only slightly visible and no annuli are obvious.

The epiotics (epo) form the dorsoposterior corners of the braincase. The two dorsolateral skull ridges extend from the frontals to the parietals and terminate abruptly at the dorsoposterior corners of the skull. The right epiotic is the ultimate dorsoposterior bone on the right side. The dorsal margin of the left epiotic is capped by a projection of the left parietal. Each epiotic presents a posterolateral facet for articulation with the posttemporal.

The opisthotics (opo) are small bony wedges between the autopterotic, exoccipital, and basioccipital. The left opisthotic features a short projection bracing the lower portion of the postemporal.

The exoccipitals (exo) contain the foramen magnum. From rear view, each exoccipital presents a triangular facet which, with the basioccipital, forms the tricondylar articulation with the atlas. One pair of ventrally directed formamina afford passage of the tenth cranial (vagus) nerve. This nerve exits through the exoccipital in all flatfish families examined by Chabanaud (1936).

The supraoccipital (soc) has a low median crest with five serrations articulating with bases of the first five dorsal pterygiophores.

The parietals (p) contact the frontals, supraoccipital, epiotics, and autopterotics. A small finger of the left parietal forms a dorsal cap over the left epiotic.

The small posttemporals (pt) connect the pectoral girdle to the skull. The uppermost portion of each rests on a flat lateroventral surface of the epiotic. The left postemporal is further braced by a projection from the episthotic. Medially, the posttemporal articulates with the supracleithrum on an expanded face.

The anteriormost of the two elements of each lateral extrascapular (les) is a tripartite ossicle serving as the junction of the temporal, supratemporal, and posttemporal sensory canals. The anterior element of the left extrascapular is not as well developed as its right counterpart. The symmetric posterior elements are fused to the posttemporals.

The basioccipital (boc) comprises the posteroventral portion of the cranium, the basal articulation of the atlas to skull, and the posteroventral wall of the auditory capsule. The suture of the basioccipital with the prootic along the parasphenoid is incomplete; a triangular piece of cartilage intervenes.

The parasphenoid (pas) is a large laterally compressed bone, traversing the length of the skull, bridging otic and olfactory regions. Anterior to its suture with the prevomer, a deep groove receives a projection of the left prefrontal complex.

In premetamorphosing larvae (Fig. 7), the parietals, autopterotics, epiotics, and posttemporals are visible. Each parietal bears a small bony ridge with either one or two spines. The autopterotics are small oval bones with a prominent knob on the center of each bone. The epiotics are vaguely discernible in the dorsoposterior aspect of the braincase. The posttemporals are tiny fusiform bones, each bearing a single spine. The basioccipital is a conical projection contiguous with the notochord, overlapping the filiform parasphenoid which extends to the olfactory region.

The autosphenotics first appear in a 2.5 mm SL larva (Fig. 8). The parietals have enlarged, and the bony ridge becomes located farther dorsad. The remaining bones of the otic and basicranial region are essentially the same as those in the 2.14 mm specimen of Fig. 7.

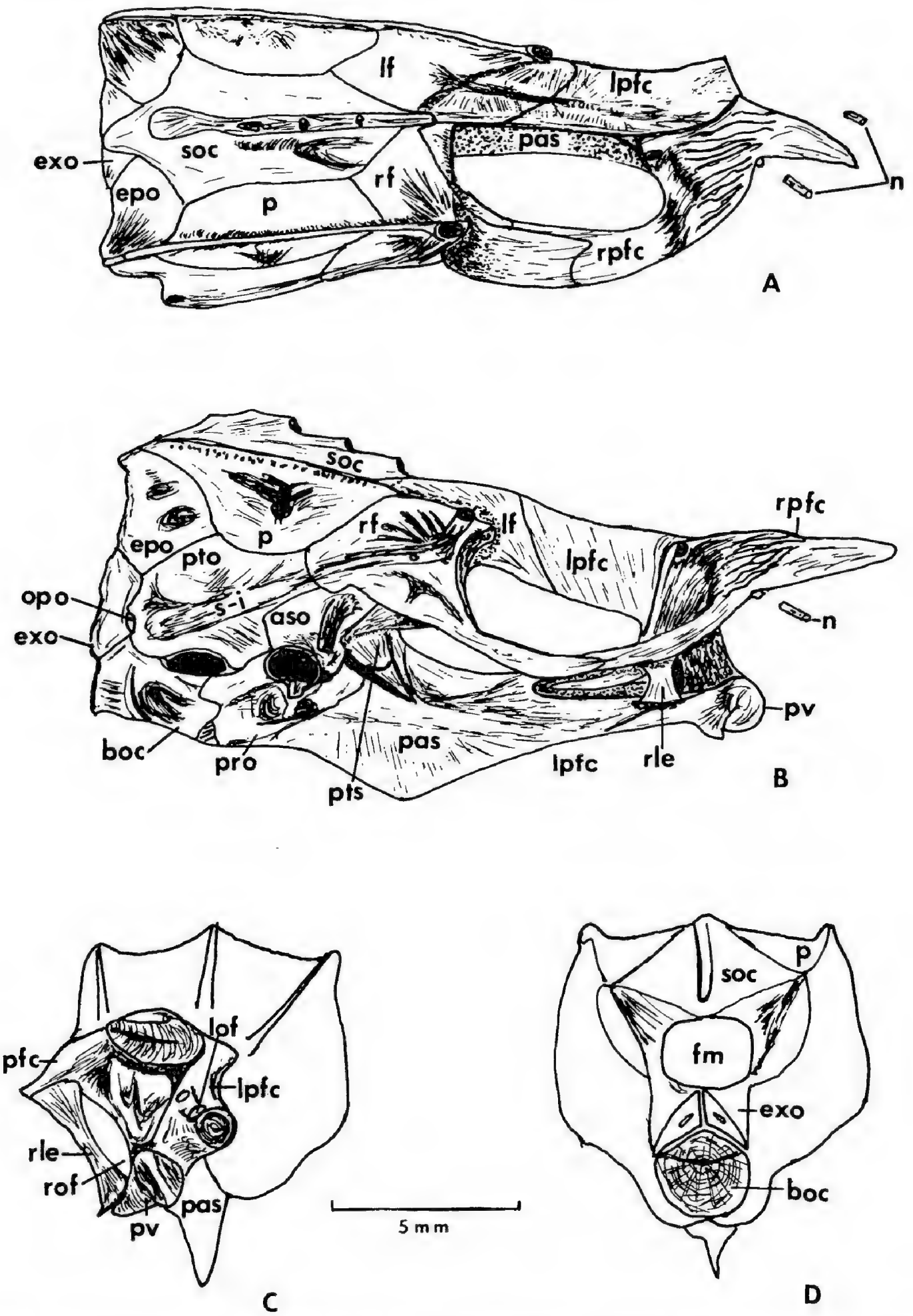

FIG. 1. Neurocranium. A, dorsal view; B, lateral view; C, anterior view; D, posterior view. Drawn from 92 mm SL specimen (FSBC 4362).

At 3.2 mm SL (Fig. 9), when eye migration has begun, all bones of the otic series are more clearly visible. The small knobs of the autopterotics become spinous bony ridges, later forming bony housings over the supratemporal-intertemporal laterosensory system. These elements are here designated the supratemporal-intertemporals, although the homology has not been demonstrated beyond question. The prootics appear posteroventral to the autopterotics. The walls of the basioccipital enclosing the auditory capsule begin to ossify. Throughout development, the parasphenoid lengthens and deepens in the sagittal plane. It becomes curved and deflected toward the right (ocular) side.

In 5 mm SL larvae, all bones of the otic region are easily distinguished, although not all are completely ossified or in obvious contact with neighboring bones. The tenth cranial nerve foramen appears at this stage. The supraoccipital becomes visible in profile as a small sliver of bone above the parietals. Although anterior dorsal pterygiophores are present, supporting serrations of the supraoccipital crest have not developed in larvae of this size.

All bones of the otic and basicranial region except the prootics had attained adult form in a 14 mm juvenile. The prootics continue to ossify anteriad toward, but never reaching, the pterosphenoids, thus forming foramina for the jugular and orbital arteries.

Some comparisons between neurocrania of *A. lineatus* and the genus *Solea* are possible. Chabanaud (1936) figured the orbital and olfactory regions of *Achirus* and *Solea*. Synonymy of Chabanaud's terms with those presented herein are as follows: ME = right prefrontal complex; PEZ = right lateral ethmoid; PEN = left prefrontal complex; FZ = right frontal; FN = left frontal; SPZ = right autosphenotic; SPN = left autosphenotic; SO = supraoccipital; and V = prevomer. *Solea* apparently has fusion of prefrontal and lateral ethmoid elements similar to that of *A. lineatus*, thus indicating that orbits of each genus are composed of the same series of bones. The autosphenotics of *Solea* are larger than their counterparts in *Achirus*, and project anteriad into the orbital region. Paired asymmetric first infraorbitals (= lacrymals) are present in *Solea solea* (Yazdani, 1969) but not in *A. lineatus*.

Otoliths of *A. lineatus* are similar to those of *S. solea*, as described and figured by Schmidt (1968). Schmidt notes an otolith length-width-depth ratio for the otoliths of *S. solea* from three specimens, 180, 300, and 370 mm in length, as 1.00/0.86/0.27. The ratio for an otolith of a 92 mm specimen of *A. lineatus* was 1.00/0.66/0.27.

BRANCHIOCRANIUM

Oromandibular Region (Figs. 2, 3, and 11)

The premaxillaries (pm) are asymmetric. The right is edentulous and short, not excluding the maxillary from the gape. Its medial ascending process (as) is broadened anteriorly, forming a deep posteromedial depression which fits the right anterior surface of a median rostral cartilage. The small articular process (ar) fits a maxillary facet. The left premaxillary, heavily toothed with sharp villiform teeth, completely excludes the maxillary from the gape. The proximal

end of the medial ascending process caps the left anterior surface of the rostral cartilage. The distal end overlies this cartilage. The articular process is received by a shallow fossa in the maxillary. Distally, the premaxillary is broadened, with a small postmaxillary process (pp) near the articulation with the maxillary.

The right maxillary (mx) bears a large proximal cranial condyle (cc) articulating with the dextrally deflected head of the prevomer. A dorsal projection, the maxillary spike (mk) articulates with the right lateral surface of the rostral cartilage. A small lateral process, the "dorsal process" of Yazdani (1969), is directed anteriad toward the premaxillary. Distally, the maxillary curves ventrad to contact the coronoid process of the dentary. The left maxillary has three proximal processes, the dorsal cranial condyle (cc), the ventral premaxillary condyle (py), and the medial maxillary spike (mk). The cranial condyle articulates with the prevomer, the premaxillary condyle receives the articular process of the premaxillary, and the maxillary spike contacts the lateral surface of the rostral cartilage. A small dorsal facet receives the ventral projection of the autopalatine head. Distally, the maxillary has a broadened end which intercedes between the premaxillary and the coronoid process of the dentary and the anterodorsal arm of the angular.

The dentaries (d) meet in mesial symphysis. The right is edentulous. Its cornoid process articulates with the maxillary, and a large lateral knob probably prevents anterior displacement of the maxillary. A medial groove receives the anterior portion of the angular (a). A perforated bony tube houses the right mandibular laterosensory canal. The anterodorsal surface of the left dentary bears sharp villiform teeth. Posteriorly, the coronoid process curves dorsad. The maxillary contacts the coronoid process and the anterodorsal arm of the angular. Ventrally, small bony arches partially enclose the left mandibular laterosensory canal. The anterior portion of the right angular is recessed in the dentary. Posteriorly, a deep fossa receives the quadrate condyle. Ventrally, the mandibular sensory canal is partially enclosed in a bony sheath. The left angular is positioned like that of the right side, but is more heavily ossified. The anterodorsal arm of the angular contributes, with the coronoid process of the dentary, a connection with the premaxillary and maxillary. The mandibular branch of the laterosensory canal is only partially enclosed in a bony housing.

The coronomeckelians (unfigured) are small chip-like bones on medial surfaces of both angulars.

The retroarticulars (rar) cap the ventroposterior corners of the angulars.

The edentulous autopalatines (ap) are the anteriormost bones of the palatoquadrate arch. Posteriorly, they are connected to the ectopterygoids and endopterygoids, contributing to the palate. The right autopalatine curves dorsally beneath a shelf formed by the right lateral ethmoid, and is connected there by cartilage. There is no point of articulation with the maxillary. The left autopalatine sends one condyle anterodorsad, making a cartilaginous connection with the left prefrontal complex. An anteroventral condyle rests in a dorsal depression in the left maxillary.

The ectopterygoids (ecpt) curve dorsoanteriad from the anterior edge of the

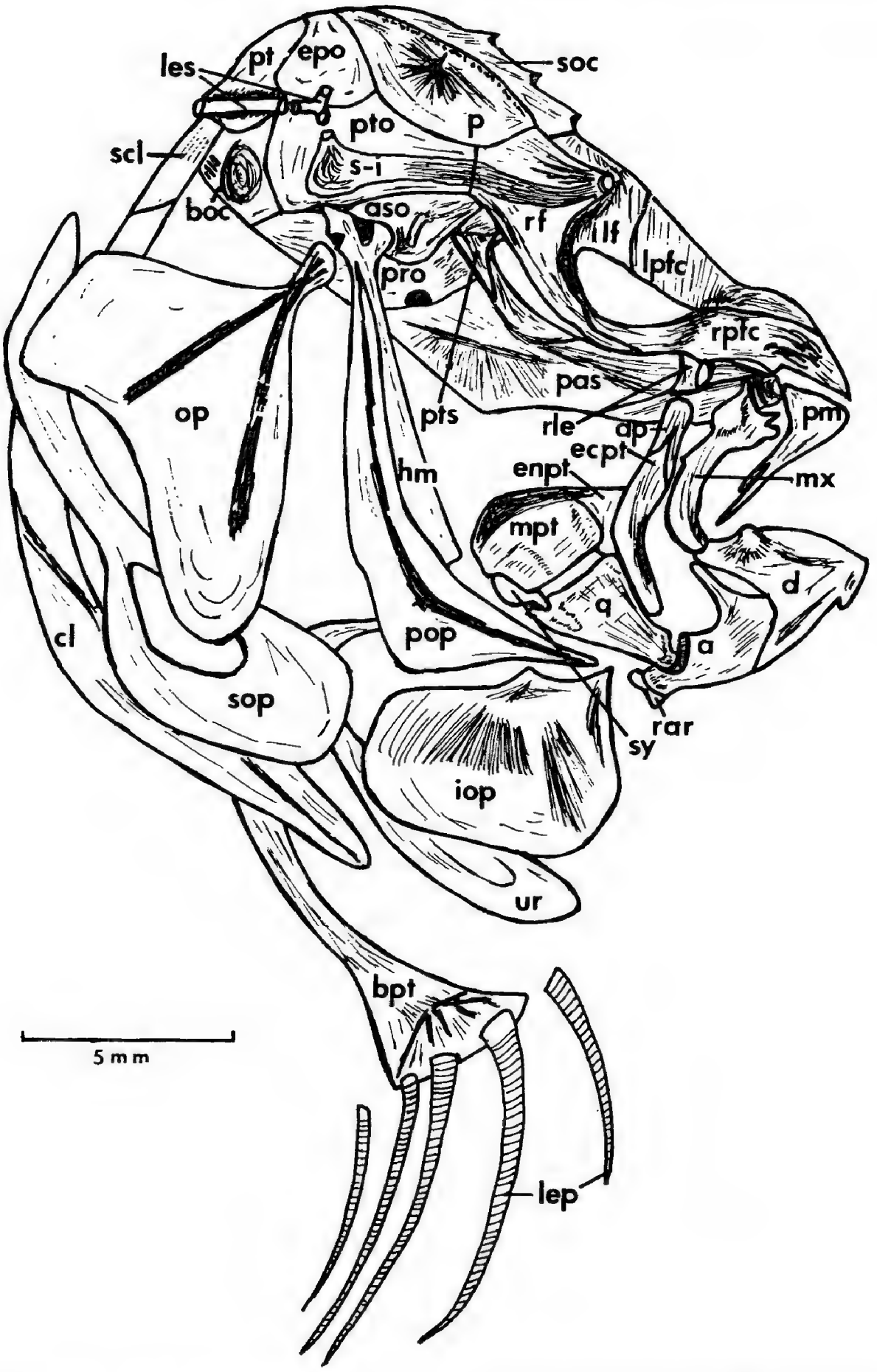

FIG. 2. Syncranium and appendicular skeleton. Drawn from 76.5 mm SL specimen (FSBC 5968).

quadrate to the autopalatines. The left ectopterygoid is longer than its right counterpart.

The endopterygoids (enpt) are roughly triangular. Their anterior margins are curved and sutured to the medial faces of the autopalatines and ectoptery-

goids. The posterior margins broadly join the anteromedial surfaces of the metapterygoids and quadrates. The dorsal margins are directed mediad, contributing to the palate.

The metapterygoids (mpt) overlap the endopterygoids anteriorly, and the symplectics posteriorly, each contributing to the palate.

The quadrates (q) are triangular in profile. The lower vertices broaden into strong tranverse condyles articulating with the angulars. A deep medial groove accommodates the lower shaft of each symplectic. The dorsal margins do not contact the metapterygoids but are joined by connective tissue.

The dentaries and angulars are the most conspicuous bones of the oromandibular series in premetamorphosing larvae (Figs. 7 and 8). They appear as lamellae arising from the anteromesially joined rami of Meckel's cartilages. Posteriorly, each angular is curved, forming a fossa to receive the quadrate condyle. Ventrally, each dentary and angular bears several spinous epidermal ridges later to become bony coverings for laterosensory canals. The posterior ends of Meckel's cartilages bend ventrad, ending in the retroarticulars. The maxillaries are small filiform bones extending from the olfactory region to the coronoid processes of the dentaries.

In early metamorphosing larvae (Fig. 10) both premaxillaries are present, and are overlapped by lateral process of the maxillaries. In 5mm SL larvae. the now dentate left premaxillary completely excludes the maxillary from the gape. Jaw structures have attained adult form on fish of about 10 mm SL.

The quadrates are visible in premetamorphosing larvae (Figs. 7 and 8). Although through ossification of the neurocranium and hyoid arch is incomplete, and bony neurocranial suspension is not effected, the cartilaginous connection between the quadrate, symplectic, and hyomandibular apparently offers sufficient resistance so that an adductor-abductor muscle system can effectively operate the jaws.

The pterygoid series and autopalatines appear when larvae are about 3 mm SL (Fig. 9). The ectopterygoids and autopalatines first appear as small curved filaments between the quadrates and the olfactory-oromandibular regions. They are always asymmetric; those of the left side are larger than those of the right. These bones, like those of the upper and lower jaws, attain adult form when fish are about 10 mm SL.

Morphology and function of the jaws of *Solea solea* and *Achirus fasciatus* (=*Trinectes maculatus*) were compared by Yazdani (1969). Lower jaws of both species and upper jaws of *S. solea* are capable of independent movement. In both, upper and lower jaws of the blind side are toothed, and are especially adapted to dislodge and consume polychaete worms, the major food item of both species. According to Yazdani (1969), the edentulous upper and lower jaws of the ocular side do not function in feeding, but open and close to allow respiratory current passage.

The jaws of *A. lineatus*, *T. maculatus*, and *S. solea* are similar although the "dorsal process" (actually a lateral process) of the maxillaries overlies the premaxillaries in *S. solea* and *T. maculatus* (Yazdani. 1969), but does not in *A. lineatus*. The lower jaws of *A. lineatus* and *T. maculatus* are similar. The left dentary of *S. solea* is smaller than that of either *A. lineatus* or *T. maculatus*. Thus,

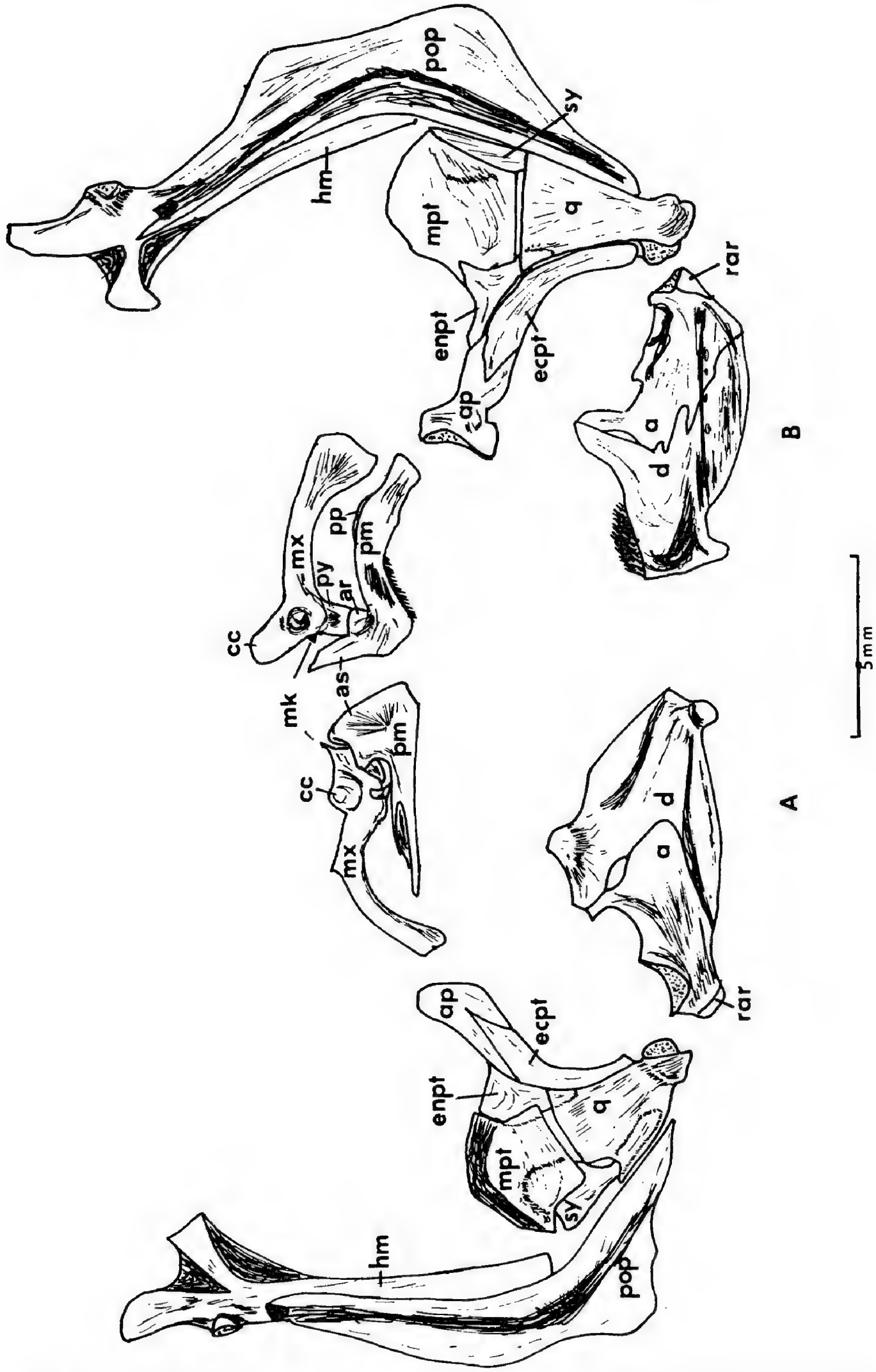

FIG. 3. Jaws and palatoquadrate arches. A, right side; B, left side. Drawn from 92 mm SL specimen (FSBC 4362).

Yazdani considers the jaws of *Trinectes* primitive with respect to the specialized lower jaws of *Solea.*

Hyoid Region (Figs. 2, 3, and 4)

The hyomandibular (hm) is a large cruciform bone forming the main attachment of the branchiocranium to neurocranium. The anterior and dorsal arms of the hyomandibular articulate with the neurocranium. The anterior arm fits into a fossa formed by the prootic and autosphenotic, and the dorsal arm lies in a deep depression on the underside of the autopterotic. The short posteriorly directed arm forms a fossa for articulation with the opercular. The long ventral arm, the symplectic process, extends ventrad to the cartilaginous attachment with the symplectic and interhyal. A depression on the lateroposterior margin of the symplectic process receives the dorsal end of the preopercular. A medial canal directs the hyomandibular branch of the facial nerve ventrad. Laterally, the hyomandibular branch of the laterosensory canal system is encased in a bony sheath.

The symplectics (sy) are two small wedges of bone fitting into a groove on the posteromedial portion of each quadrate. They expand dorsally and are partially overlain by each metapterygoid. The left symplectic has broad contact with the leading edge of the preopercular, but the right symplectic does not contact the right preopercular.

The interhyal (ih) is a small rod-like bone fitting into the cartilaginous connection between the symplectic and the symplectic process of the hyomandibular. Ventrally, it attaches near the posterodorsal border of the epihyal.

The epihyal (eh) is a broad quadrangular bone inseparably joined to the ceratohyal by strong odontoid processes across medial faces of both bones. Because homology of the epihyal is uncertain (McAllister, 1968; Nelson, 1969), we prefer generally accepted terminology, as suggested by McAllister. The epihyal supports three branchiostegals.

The ceratohyal (ch) is a broad semicircular bone with a stout anterior ramus. Above and below this ramus are attached the upper and lower hypohyals. Four branchiostegals are supported by the ceratohyal.

The upper hypopyal (uhh) fits dorsally onto the anterior ramus of the ceratohyal. It has a concave face fitting between the junction of the basibranchial and first hypobranchial. A small medial foramen pierces each upper hypohyal.

The lower hypohyal (lhh) caps the anteromedial end of the ceratohyal.

The basihyal (bh) is a median flattened bone, rounded posteriorly, forming the base of the tongue.

The urohyal (ur) is an intramembranous ossification lying beneath the basibranchial elements. Its anterior end lies in the hypohyal region. Posteriorly, it deepens in the sagittal plane, and curves ventrad. Its posterior margin is adjacent to the anterior margins of the cleithra.

The seven pairs of acinaciform branchiostegals (b) increase in size, proceeding posteriad. Four are attached to the ceratohyal, and three to the epihyal. Occasionally, one side may have only six branchiostegals.

The second through fifth branchiostegals have broad anteriorly directed proc-

esses which overlap adjacent branchiostegals, giving extra support to gill membranes. The first branchiostegal of each side is in mesial contact with its fellow, as in other Soleidae (McAllister, 1968).

The preopercular (pop) is a large crescentic bone following the suspensorial curve. Its leading edge partially covers the symplectic process of the hyomandibular, and ends posterolaterally in a hyomandibular sulcus. The trailing edge is thin, with a prominent bulge at the angle. The laterosensory canal from the temporal to the mandibular region is completely encased within the preopercular.

The opercular (op) is a broad, thin triangular bone. The posteriorly directed fossa of the hyomandibular articulates with the opercular condyle. The opercular condyle is continguous with two thickened ridges, one directed posteriad, the other ventrad, the latter comprising the opercular leading edge.

The subopercular (sop) is a long thin bone extending from the angle of the preopercular to a point above the opercular. It is ventrally broadened, but narrows abruptly about at its midpoint. The ventral corner of the opercular rests in an elliptical aperture in the subopercular. In older specimens, this aperture becomes completely ossified.

The interopercular (iop) is a heavy quadrangular bone lying below the preopercular and sutured to the epihyal.

The sympectics and hyomandibulars are conspicuous in premetamorphosing larvae (Figs. 7 and 8). The branchiostegals develop as small filiform rods emanating from the epihyal and ceratohyal cartilages. When larvae are about 2.5 to 3.2 mm SL, the full complement of branchiostegals is usually present.

In 3.2 mm SL larvae (Fig. 9), the interhyal is visible between the epihyal and the cartilage intervening between the symplectic and hyomandibular. In juveniles of about 10 mm SL, the hyoid and branchial arches may be dissected from the neurocranium.

At 10 mm SL, the ceratohyal is incompletely sutured to the epihyal and perforated by a large foramen, the "beryciform foramen . . . found in the beryciforms and some of their derivatives" (McAllister, 1968). Accordingly, he proposed that presence of this foramen in some adult members of the order indicates a preperciform origin of Pleuronectiformes. In adult *A. lineatus*, only a small depression is present as a remnant of this foramen.

Opercular elements are present in premetamorphosing larvae (Fig. 7 and 8). The opercular is a small Y-shaped ossification directed posteriad from the posterior arm of the hyomandibular. The preopercular is a small crescentic bone at the angle of the hyomandibular and symplectic. It bears three or four epidermal spines, later to become the bony covering for a laterosensory canal. The interopercular is a tiny oval bone bearing two epidermal spines, located ventral to the preopercular and posterior to the symplectic. During development, the Y-shaped bifurcation of the opercular widens, and ossification occurs between the rami. The preopercular maintains its crescentic configuration and grows dorsad and ventrad. The interopercular broadens ventrally to assume the adult form. Formation of all bones of the opercular series is essentially complete by 14 mm SL.

Branchial Region (Fig. 4)

Following Topp and Cole (1968), "the terms 'proximal' and 'distal' are used with respect to the neurocranium; 'abpharyngeal' and 'adpharyngeal' are used in respect to the pharyngeal cavity."

The ventromesial basibranchials (bb) are located in the floor of the pharynx. The first basibranchial is a triangular bone resting between the upper hypohyals and posterior to the basihyal. The second basibranchial is spatulate; the heavy body of the bone is hourglass-shaped, with the widest part posterior. Laterally, thin lamellae complete the spatulate profile. The third basibranchial is a long bone posterior to the second basibranchial.

The first hypobranchial (hb) is a quadrangular bone articulating distally with the first and second basibranchials, and proximally with the first ceratobranchial. The similar second hypobranchial articulates distally with the second and third basibranchials, and proximally with the second ceratobranchial. The third hypobranchial is square, the anterior vertex bearing a strong ventral process. This element connects distally with the third basibranchial, and proximally with the third ceratobranchial.

The first four ceratobranchials (cb) are similar, but decrease in size posteriorly. Each has a small abpharyngeal groove for conduction of branchial blood vessels. The first four have proximal cartilaginous attachments to their respective epibranchial elements. The first three articulate distally with the three basibranchials. The fourth ceratobranchials have no ossified distal support. The fifth ceratobranchials (lower pharyngeal toothplates of Nelson, 1969) bear sharp villiform, dorsally directed teeth. The fifth ceratobranchials have no circumpharyngeal elements.

The four epibranchials (eb) angle anterodorsad from the cartilaginous connections with their corresponding ceratobranchials, the blood vessels continuing in abpharyngeal grooves. The first are slender rods with truncate projections directed dorsad. The slightly S-shaped second epibranchials are still shorter, each bearing a lateroposterior process involved in the insertion of the external *levatores arcuum branchialum* (Branson, 1966). The third epibranchials bear small proximal tooth plates. The fourth epibranchials are slightly curved.

Confusion exists regarding homology and terminology of pharyngobranchial elements and associated tooth plates (Nelson, 1968, 1969). We, therefore, follow generally accepted terminology (Topp and Cole, 1968).

The first pharyngobranchials (pb) are small rods directed dorsad from proximal ends of the first ceratobranchials. They are apparently involved in suspension of the branchiocranium from the neurocranium. The second pharyngobranchials are ovate, each with a small dorsal projection. Their adpharyngeal surfaces bear tooth plates with curved villiform teeth. The third pharyngobranchials, the largest of the series, are roughly triangular, each with an anterior projection and adpharyngeal tooth plate. The fourth pharyngobranchials are slender dentate bones adjacent to the posterior margin of the third. Nelson (1969) believes this element to be "purely dermal in origin, corresponding to the fourth upper pharyngeal plate . . ."

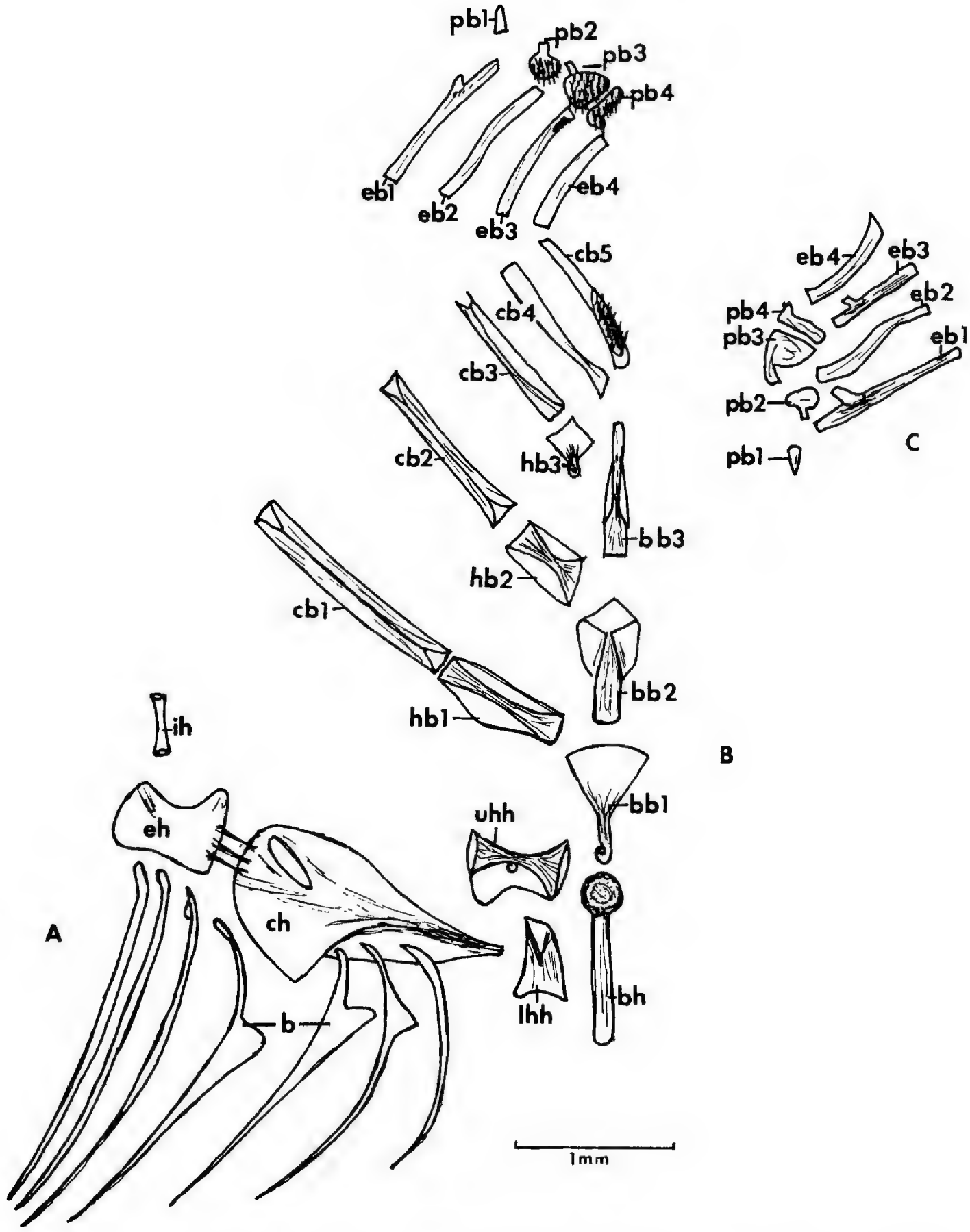

FIG. 4. Hyoid and branchial arches. A, right hyoid arch; B, adpharyngeal view; C, abpharyngeal view of upper elements. Drawn from a 10.2 mm SL specimen (FSBC 5969).

In premetamorphosing larvae, cerato- and epibranchial elements are visible as cartilage, or as very poorly ossified elements. In early metamorphosing larvae about 3.2 mm SL (Fig. 9) these elements, as well as basibranchials and hypohyals, are visible. The upper pharyngeal and fifth ceratobranchial teeth are well developed and, at this stage, probably compensate for poor jaw dentition.

VERTEBRAL COLUMN

The vertebral column (Figs. 5 and 11) consists of 9, sometimes 8 track vertebrae (tv) and 18, or less often 17, caudal vertebrae (cv) including the urostylar vertebra. No ribs are present in *A. lineatus*, nor in other soleids (Norman, 1966). In general, the elements resemble those in perciform fishes.

The first vertebra (atlas) is a short disk-shaped centrum with two anterodorsal condylar surfaces which, with the concave centrum below, form the tricondylar attachment to the skull. The paired elements forming the neural arch are autogenous, each articulating with the centrum by a bipedal facet. The two elements are joined to the second neural arch by connective tissue, but do not meet dorsomesially.

The second vertebra (axis) bears a lateral apophysis located well above the midline of the centrum. This apophysis has a bony laminar connection to a small posterodorsal knob, representing the neural prezygapophysis, which forms a shelf for the lateral facet of the autogenous first neural arch. The wide base of the neural arch expands posteriorly to form a large neural postzygapophysis. The anterior profile of the neural arch is slightly concave to accommodate the first neural elements. The straight portion of the neural spine is joined to the supraoccipital by connective tissue (in Fig. 11 the first and second neural spines are obscured by the posttemporal).

The lateral apophysis of the third centrum is slightly above the axial midline. The small neural prezygapophysis is located almost directly above the lateral apophysis, and articulates with the neural postzygapophysis of the second vertebra. The third neural arch sends back a strong postzygapophysis. The neural spine is strongly curved forward.

The lateral apophysis of the fourth trunk vertebra is directly on the midline of the centrum and is the most developed of any on the entire column. The neural arch and spine incline forward.

The fifth trunk vertebra bears a lateral apophysis below the central midline. The neural prezygapophysis is very prominent. Paired parapophyses meet ventrally to form the first hemal arch. The neural arch and spine are strongly bowed anteriad.

The sixth through ninth trunk vertebrae possess consecutively less prominent lateral apophyses. Caudal vertebral apophyses are represented only by curvatures in central margins. The neural prezygapophyses become increasingly prominent in trunk vertebrae and parapophyses increase in length. The neural arches and spines are angled anteriad.

The first caudal vertebra has an exceedingly large hemal spine, its anterior face deeply grooved to accommodate the first anal pterygiophore.

Proceeding posteriad, caudal vertebrae reduce in size. Neural and hemal components of the first caudal vertebra are approximately vertical, becoming posteriorly directed in successive vertebrae.

The last three vertebrae are modified for caudal fin support.

Development of the vertebral column proceeds posteriad. The first neural elements appear on the trunk vertebrae of premetamorphosing larvae (Figs. 7 and

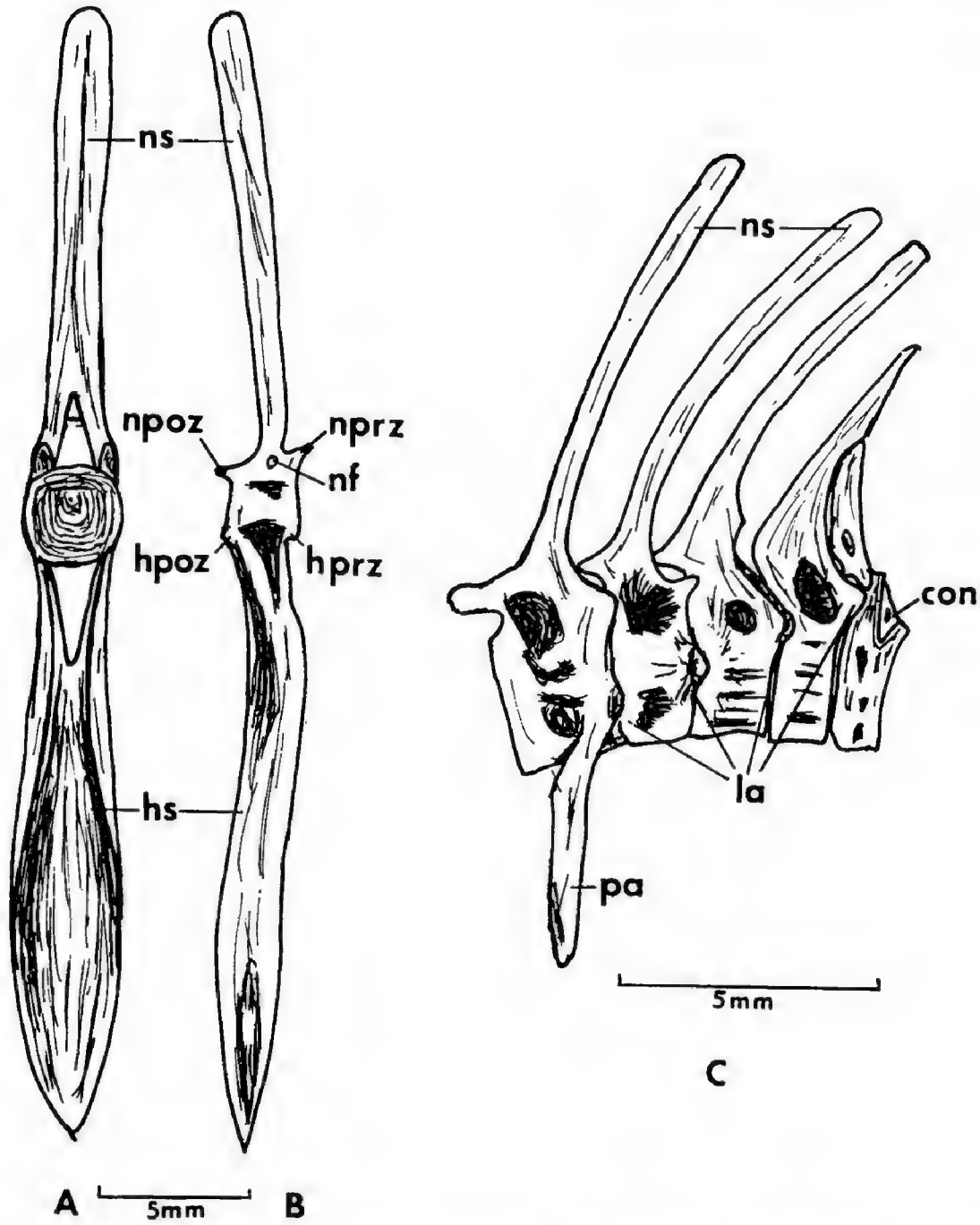

FIG. 5. A, anterior view of first caudal vertebra; B, lateral view of first caudal vertebra; C, first through fifth (right to left) trunk vertebrae. Drawn from 92 mm SL specimen (FSBC 4362).

8) as small filaments of bone arising from lateral surfaces of indistinct arcualia. The remainder of the vertebral column is undifferentiated. The full complement of vertebrae is attained by larvae between 2.5 and 3.0 mm SL (Fig. 9). At this size, the posterior end of the notochord, later to becofe the urostylar vertebra, is flexed dorsad. During antogeny, intervertebral cartilages become much reduced, and vertebrae become more closely approximated.

Although axial skeleton structure of *A. lineatus* is similar to that of *S. solea* as described by Ford (1937), the two differ greatly in numbers of caudal vertebrate; *S. solea* has 40, *A. lineatus* 17 or 18. Trunk vertebrae of the two are almost identical. The first neural spine of *S. solea* is not closed to form a complete arch (Ford, 1937). Further, his photographs show that neural elements of the first vertebra are attached to the second neural arch and that the second neural spine contacts the supraoccipital, as in *A. lineatus*. A similar configuration is present in *S.*

vulgaris (Kyle, 1921). *S. solea* and *A. lineatus* each have five trunk vertebrae with parapophyses meeting ventromesially to form hemal arches. Lateral apophyses are different, however. They extend throughout the vertebral column in *S. solea* but are obvious only on the second through fifth vertebrae of *A. lineatus*.

CAUDAL SKELETON

The caudal skeleton resembles in essential respects that described by Gosline (1961) as primitive among perciform fishes. Gosline established the rationale for numbering hypural elements from ventral to dorsal. For convenience, we advocate numbering caudal lepidotrichs in the same manner.

The hemal spine of the antepenultimate (25th) vertebra is longer and heavier than its preceding counterpart, and supports one or more lepidotrichs. The neural spine does not enter into caudal fin support. The autogenous hemal spine of the penultimate (26th) vertebra is long and deepened in the sagittal plane. It supports the second, and sometimes part of the first lepidotrich.

The proximal ends of hypurals 1–4 originate from the ventral and posterior margins of the urostylar vertebra; the fifth arises above the tip. Hypurapophyses (Nursall, 1963) are absent.

The single parhypural (*sensu* Monod, 1968) is proximally adjacent to the autogenous 26th hemal spine. It typically supports the third, fourth, and part of the fifth lepidotrichs.

The single epural lies adjacent and posterior to the neural spine of the 26th vertebra. It typically supports the 15th and part of the 16th lepidotrichs.

Caudal fin elements appear in larvae about 2.5 mm SL (Fig. 8), although the posterior section of the notochord is undifferentiated and straight. Four cartilaginous elements are located on the posteroventral surface of the notochord. In metamorphosing larvae (Fig. 9), the last three vertebrae are undifferentiated from the dorsally flexed notochord, but neural and hemal spines of the 25th and 26th vertebrae are visible. The parhypural also arises immediately posterior to the 26th hemal spine. Four hypurals arising from the ventral surface of the urostylar vertebra are present.

In more advanced larvae (Fig. 10), the last three vertebrae are distinct. The parhypural is definitely associated with the 26th vertebra. In the adult, it may be located such that it appears to have arisen from the urostylar vertebra, and might mistakenly be considered a hypural. Its true origin from the 26th vertebra is shown during ontogeny.

The fifth hypural develops dorsal to the urostylar vertebral tip in metamorphosing larvae, all caudal elements being present at this stage (Fig. 10). Increased ossification, and some fusion of caudal elements occur in older specimens.

The caudal skeleton of *S. solea*, as described by Monod (1968), is remarkably similar to that of *A. lineatus*.

MEDIAL FINS

Considerable variation exists in dorsal and anal fin ray counts. Jordan and Evermann (1898) list: dorsal, 49–58, and anal, 38–44. Although numbers vary,

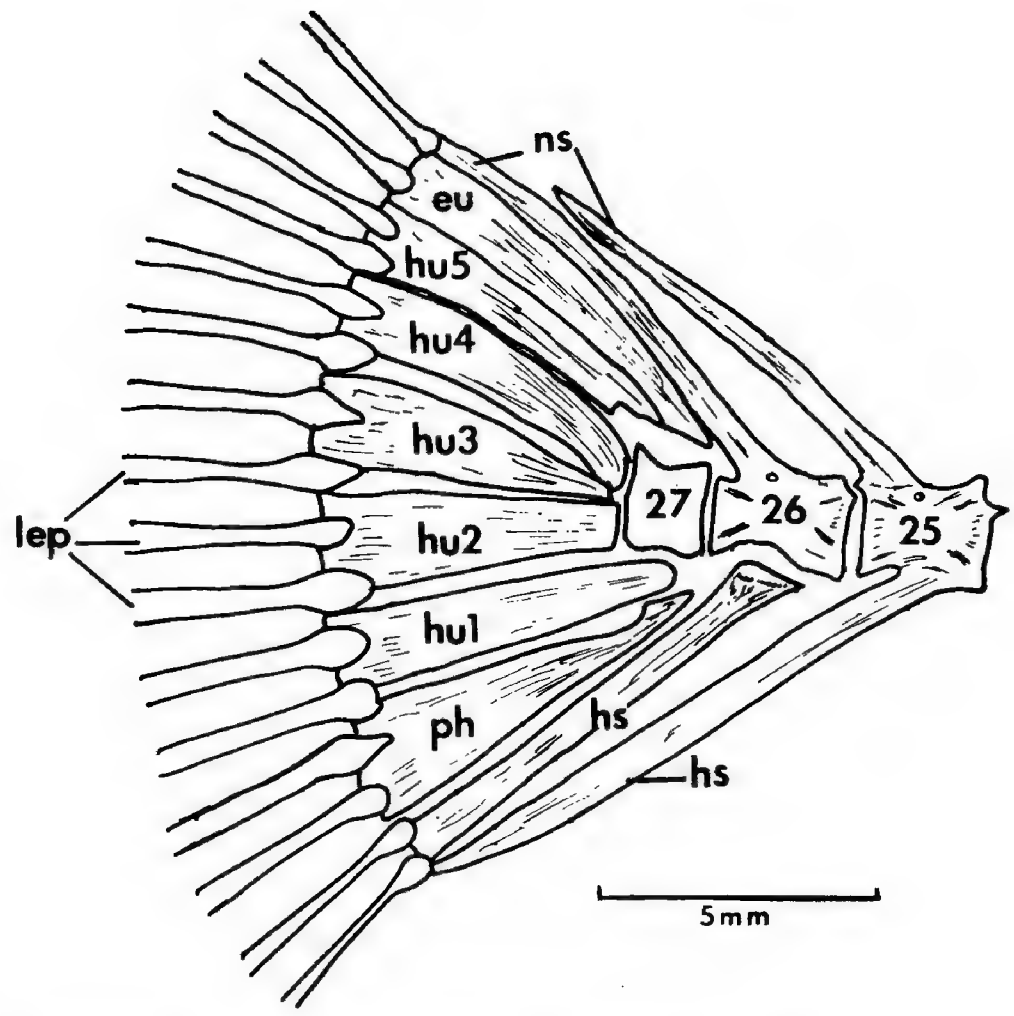

FIG. 6. Caudal fin. Drawn from 76.5 mm SL specimen (FSBC 5968).

basic triserial structure of fins is uniform. Basic median fin structure of the type encountered in *A. lineatus* is adequately discussed by Topp and Cole (1968).

The first and second (anterior) lepidotrichs of the dorsal fin are supported by one pterygiophore whose base rests in the anterior-most notch of the supraoccipital crest. Proximal bases of the next four pterygiophores have similar cranial support. The sixth interdigitates with the cranium and third neural spine. The proximal bases of the posterior three dorsal fin lepidotrichs have no neural connection.

Anal fin morphology is similar to that of the dorsal fin. The first (anterior) anal pterygiophore is a massive shaft of bone curving anteriorly from its proximal base set in the deeply grooved anterior face of the first caudal hemal spine. Ventrally, it presents facets for two lepidotrich attachments. This large bone, the "abdominal rod" of Kyle (1921) and Woolcott et al. (1968), and the "interhemal spine" of Norman (1934), should be properly termed "first anal pterygiophore" because of its obvious homology. Four pterygiophores arise from the grooved ventroposterior surface of the first anal pterygiophore. The posterior four anal pterygiophores occur between but do not interdigitate with, hemal spines of the 23rd and 24th vertebrae.

Development of median fins of *A. lineatus* discussed by Houde et al. (1970) may be summarized. The first median fin structures to develop are the dorsal fin pterygiophores. These appear in larvae between 2.1 and 2.4 mm SL, with anal pterygiophores developing shortly thereafter. Development proceeds posteriad.

The full complement of dorsal and anal rays is attained by individuals about 12 mm SL.

APPENDICULAR SKELETON

Loss and reduction of pectoral elements is characteristic of Soleidae. The right pectoral fin of *A. lineatus* consists of four to six small lepidotrichs without bony connection to the pectoral girdle. The left pectoral fin is absent.

The cleithrum (cl), the largest bone of the girdle, consists of dorsal and ventral limbs of equal length forming an angle of about 100°. The cleithra meet in ventromesial symphysis.

The supracleithrum (scl) fits into a shallow dorsolateral depression on the cleithrum and into a ventromedial facet of the posttemporal, connecting the two.

A postcleithrum (pcl), a tubular structure extending posteroventrad from the angle of the cleithum, occurs only in premetamorphosing and metamorphosing larvae (Figs. 7, 8, and 9) but atrophies during metamorphosis. Postcleithra are absent in adult soles (Norman, 1966).

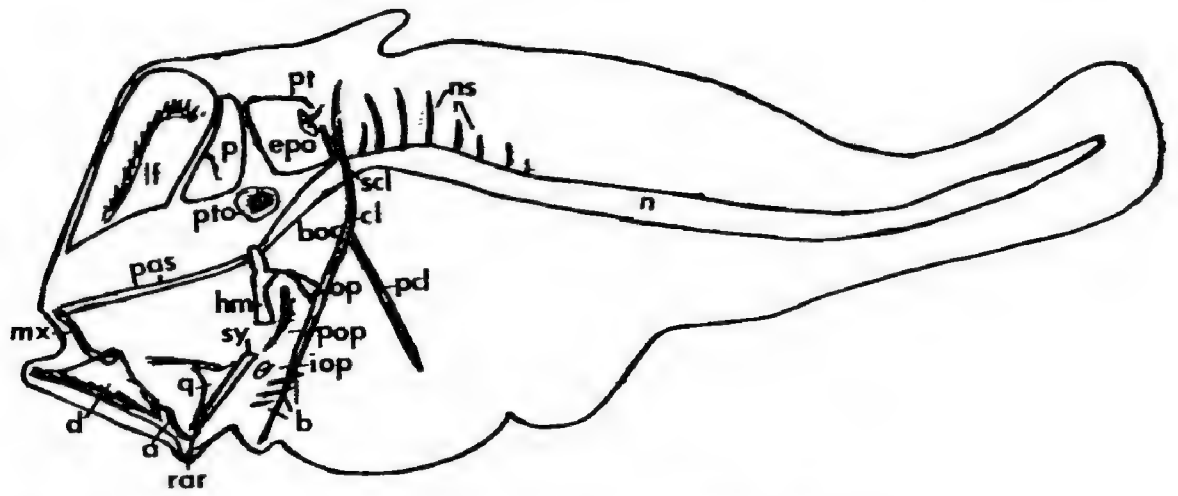

FIG. 7. Skeleton. Drawn from 2.14 mm SL specimen (FSBC 5865L).

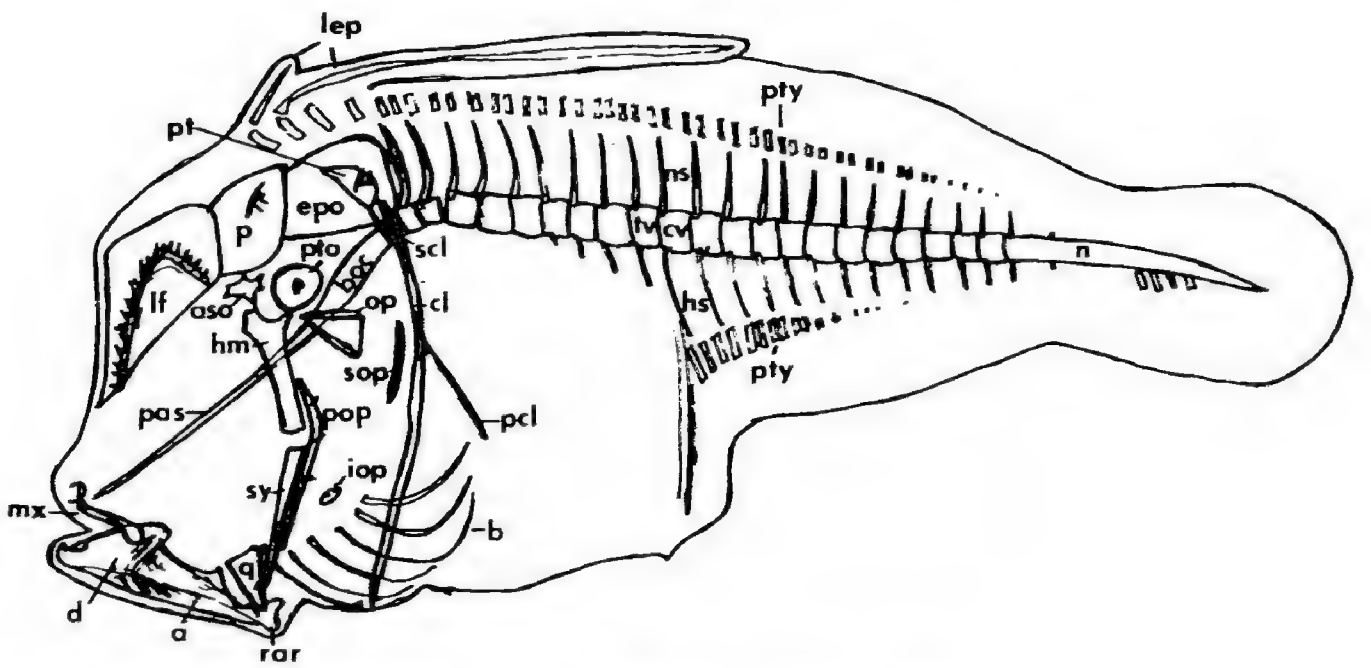

FIG. 8. Skeleton. Drawn from 2.52 mm SL specimen (FSBC 5880L).

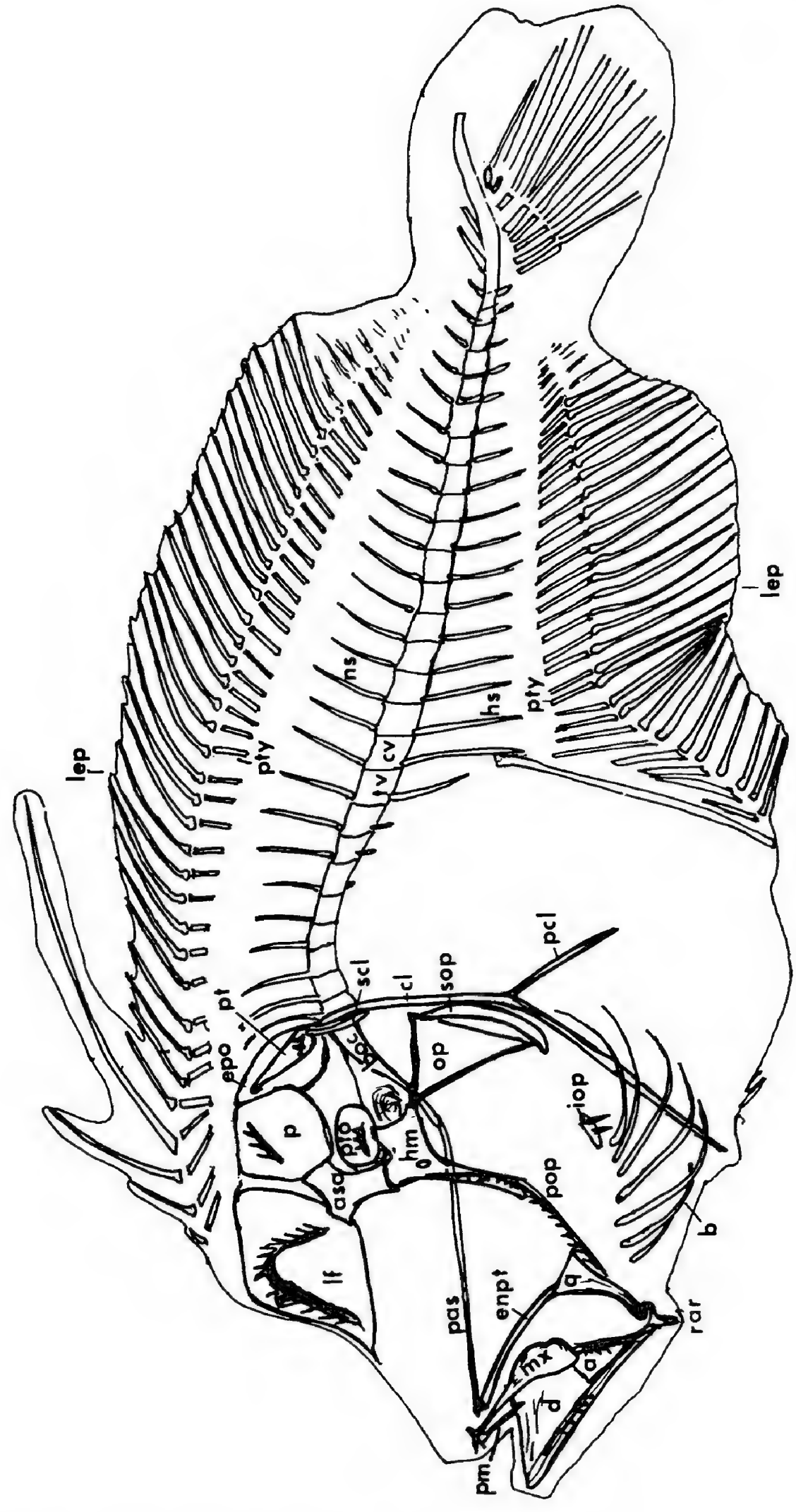

FIG. 9. Skeleton. Drawn from 3.20 mm SL specimen (FSBC 5850L).

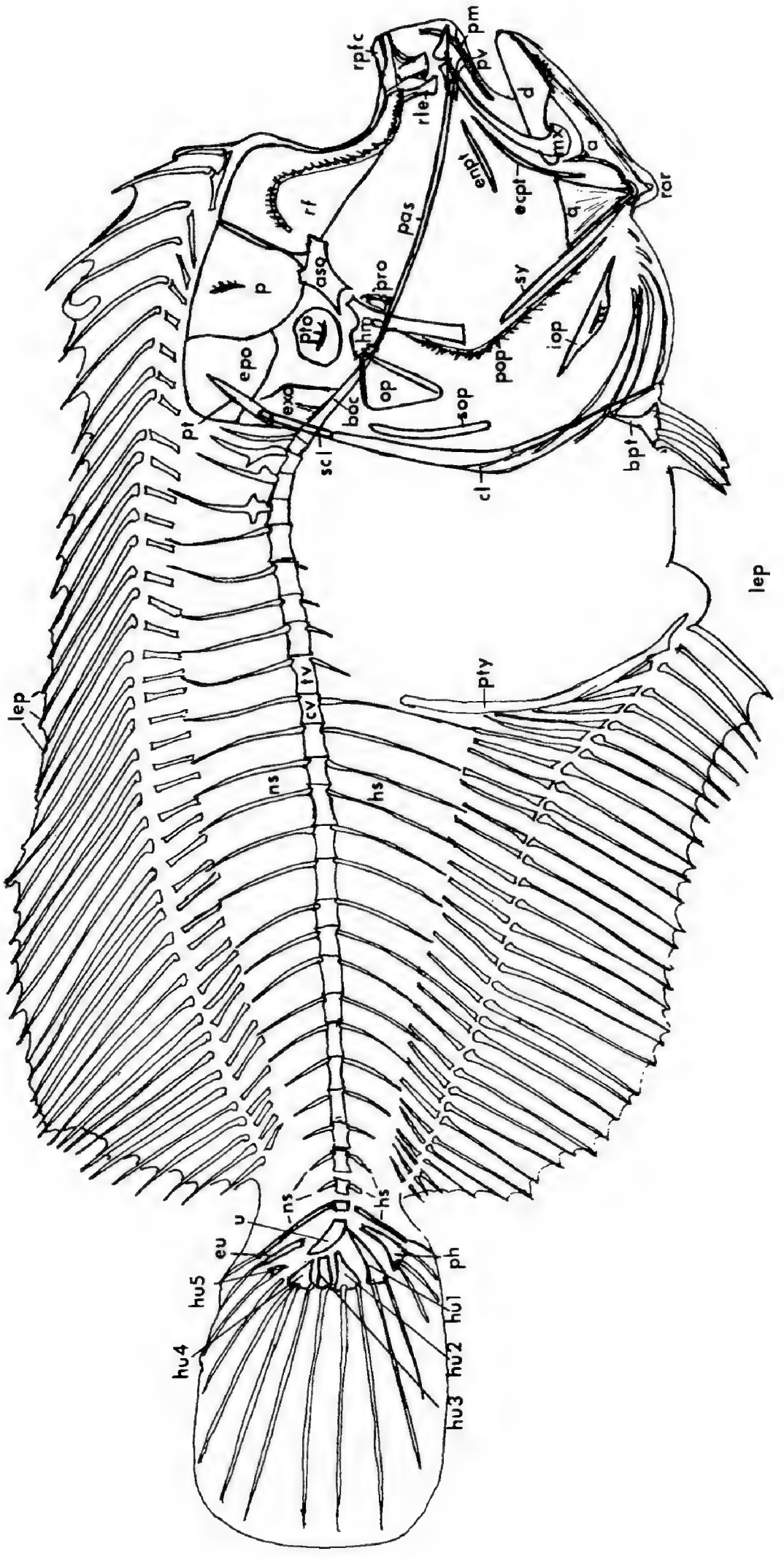

FIG. 10. Skeleton. Drawn from 3.57 mm SL specimen (FSBC 5860L).

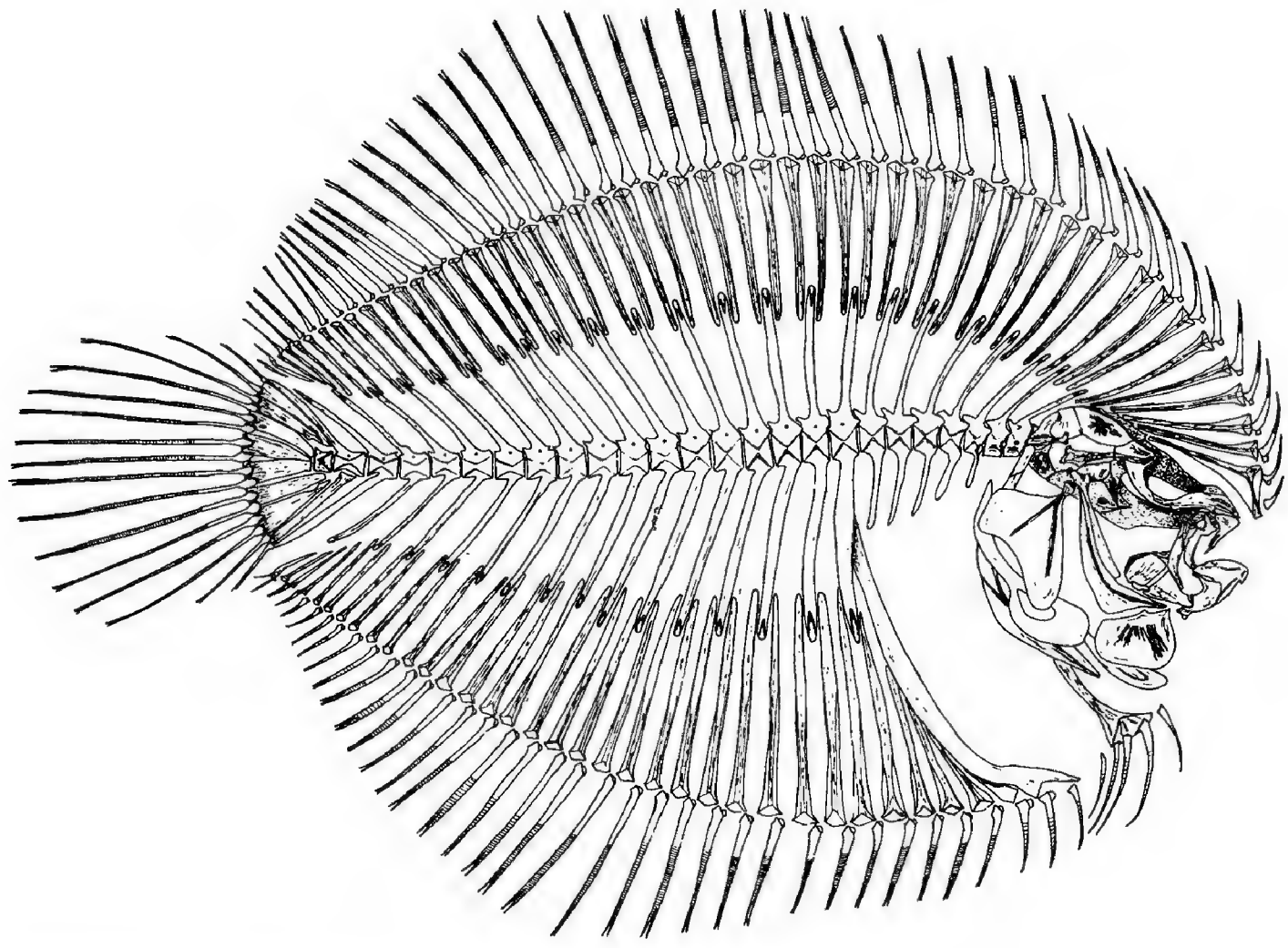

FIG. 11. Skeleton. Drawn from 76.5 mm SL specimen (FSBC 5968).

The basipterygia (bpt) are thin, sagittally flattened shafts of bone ending ventrally in broad triangular expansion. The proximal ends of the shafts are connected by ligaments to the cleithra near their ventromesial union. The ventral triangular surface supports three lepidotrichs; the first and last are free (Fig. 2).

Development of paired fins discussed by Houde et al. (1970) may be summarized. The pectoral fins of larvae have a cartilaginous base. No rays are present in larvae about 4.5 mm SL. The right pectoral fin assumes adult form by about 8 mm SL. The left pectoral is present in larvae, but atrophies and usually disappears in fish of 5 to 6 mm SL.

LITERATURE CITED

BERG, L. S. 1940. Classification of fishes both recent and fossil. *Trudy zool. Inst., Leningr.* **5**(2): 1–517.

BRANSON, B. A. 1966. Guide tothe muscles of bony fishes, excluding some special fibers in siluroids and a few others. *Turtox News* **44**:(4): 98–102.

CHABANAUD, P.M. 1936. Le neurocrane osseaux des Teleosteens dyssymetriques apres la metamorphose. *Annls. Inst. oceanogr., Monaco* **16**: 223–298.

FORD, E. 1937. Vertebral variation in Teleostean fishes. *J. mar. biol. Ass. U. K.* **22**(1): 1–60.

GOODRICH, E. S. 1958. Studies on the structure and development of vertebrates. Reprint Edition, Dover Publ. Inc., New York, pp. 1–837.

GOSLINE, W. A. 1961. The perciform caudal skeleton. *Copeia* **1961**(3): 265–270.

GREGORY, W. K. 1933. Fish skulls; a study of the evolution of natural mechanisms. *Trans. Am. phil. Soc.* **23**: 75–481.

HOLLISTER, G. 1934. Clearing and dyeing fish bone for study. *Zoologica, N.Y.* **12**: 89–101.

HOUDE, E. D., C. R. FUTCH, and R. DETWYLER. 1970. Development of larvae of the lined sole, *Achirus lineatus*, described from laboratory reared and Tampa Bay specimens. *Fla. Dept. Nat. Resources Mar. Res. Lab. Tech. Ser.* **62**: 1–43.

JORDAN, D. S. and B. W. EVERMANN. 1898. The fishes of North and Middle America. *Bull. U. S. natn. Mus.* **47**(2): 1241–2183.

KYLE, H. M. 1921. The asymmetry, metamorphosis and origin of flat-fishes. *Phil. Trans. R. Soc.* Ser. B. **211**: 75–125.

McALLISTER, D. E. 1968. The evolution of branchiostegals and associated opercular, gular, and hyoid bones, and the classification of teleostome fishes, living and fossil. *Bull. natn. Mus. Can.* 221. Biol. Ser. **77**: 1–239.

MONOD, T. 1968. Le complexe urophore des poissons Teleosteens. *Mem. Inst. fr. Afr. noire.* **81**: 1–705.

NELSON, G. J. 1968. Gill-arch structure in *Acanthodes*. *In T.* Ørvig (ed.) Current problems of lower vertebrate phylogeny. *Nobel Symposium* **4**, Stockholm.

————. 1969. Gill arches and the phylogeny of fishes with notes on the classification of vertebrates. *Bull. Am. Mus. nat. Hist.* **141**(4): 477–552.

NORMAN, J. R. 1934. *A systematic monograph of the flatfishes* (*Heterosomata*). Brit. Mus., Lond., 1–459.

————. 1966. *A draft synopsis of the orders, families, and genera of recent fishes and fish-like vertebrates.* Brit. Mus., Lond., 1–649.

NURSALL, J. R. 1963. The hypurapophysis, an important element of the caudal skeleton. *Copeia* **1963**(2): 458–459.

OSSIAN, C. E. 1970. Preparation of disarticulated skeletons using enzyme-based laundry "presoakers". *Copeia* **1970**(1): 199–200.

PATTERSON, C. 1964. A review of the mesozoic acanthopterygian fishes, with special reference to those of the English chalk. *Phil. Trans. R. Soc.* Ser. B **247**(739): 213–482.

SCHMIDT, W. 1967. Vergleichend morphologische studie uber die otolithen mariner Knochenfishe. *Arch. FischWiss.* **19**(1): 1–96.

TAYLOR, W. R. 1967. An enzyme method of clearing and staining vertebrates. *Proc. U. S. natn. Mus.* **122**: 1–17.

TOPP, R. W. and C. F. COLE. 1968. An osteological study of the sciaenid genus. *Sciaenops* Gill (Teleostei, Sciaenidae). *Bull. mar. Sci.* **18**(4): 902–945.

WOOLCOTT, W. S., C. BEIRNE, and W. M. HALL, JR. 1968. Descriptive and comparative osteology of the young of three species of flounders, genus *Paralichthys*. *Chesapeake Sci.* **9**(2): 109–120.

YAZDANI, G. M. 1969. Adaptation inthe jaws of flatfish (Pleuronectiformes). *J. zool.* Lond., **159**: 181–222.

LIST OF ABBREVIATIONS

Neucrocranium

Olfactory Region

lof	left olfactory foramen
lpfc	left prefrontal complex
n	nasal

rle	right lateral ethmoid
rof	right olfactory foramen
rpfc	right prefrontal complex
pv	prevomer

Orbital Region

lf	left frontal
pts	pterosphenoid
rf	right frontal

Otic and Basicranial Region

aso	autosphenotic
boc	basioccipital
epo	epiotic
exo	exoccipital
fm	foramen magnum
les	lateral extrascapular
opo	opisthotic
p	parietal
pas	parasphenoid
pro	prootic
pt	posttemporal
pto	autopterotic
s-i	supratemporal-intertemporal
soc	supraoccipital

Branchiocranium

Oromandibular Region

a	angular
ap	autopalatine
ar	articular process of premaxillary
as	ascending process of premaxillary
d	dentary
ecpt	ectopterygoid
enpt	endopterygoid
mk	maxillary spike
mpt	metapterygoid
mx	maxillary
pm	premaxillary
pp	postmaxillary process of premaxillary
py	premaxillary condyle of maxillary
q	quadrate
rar	retroarticular

Hyoid Region

b	branchiostegal
bh	basihyal
ch	ceratohyal
eh	epihyal
hm	hyomandibular
ih	interhyal
iop	interopercular
lhh	lower hypohyal
op	opercular

pop	preopercular
uhh	upper hypohyal
ur	urohyal
sop	subopercular
sy	symplectic

Branchial Region

bb	basibranchial
cb	ceratobranchial
eb	epibranchial
hb	hypobranchial
pb	pharyngobranchial

Vertebral Column

con	condylar surface
cv	caudal vertebra
hpoz	hemal postzygapophysis
hprz	hemal prezygapophysis
hs	hemal spine
la	lateral apophysis
n	notochord
nf	nerve foramen
npoz	neural postzygapophysis
nprz	neural prezygapophysis
ns	neural spine
pa	parapophysis
tv	trunk vertebra

Median Fins

lep	lepidotrich
pty	pterygiophore

Caudal Skeleton

eu	epural
hu	hypural
lep	lepidotrich
ph	parhypural

Appendicular Skeleton

bpt	basipterygium
cl	cleithrum
lep	lepidotrich
pcl	postcleithrum
scl	supracleithrum

DIURNAL VARIATION IN FATTENING RESPONSE TO PROLACTIN TREATMENT IN TWO CYPRINODONTID FISHES, *CYPRINODON VARIEGATUS* AND *FUNDULUS SIMILIS*

Victor L. de Vlaming and Martin Sage

University of Texas Marine Science Institute, Port Aransas, Texas 78373

ABSTRACT

There is a diurnal variation in lipogenic response to injections of ovine prolactin in two cyprinodontid fishes, *Cyprinodon variegatus* and *Fundulus similis*. Injections of prolactin eight hours after the beginning of the photoperiod cause fattening, whereas injections given two hours after the beginning of the light period cause lipid catabolism. Prolactin injections cause changes in lipid metabolism regardless of whether control fish are increasing or decreasing fat stores.

INTRODUCTION

Meier and his co-workers (Lee and Meier, 1967; Meier and Davis, 1967; Meier, 1969 and 1970) have shown a diurnal lipogenic (fat deposition) response to mammalian prolactin in teleosts, amphibians, reptiles and birds. Mehrle and Fleming (1970) also reported a diurnal variation in the lipogenic response to prolactin in *Fundulus kansae*, though Zipser *et al.* (1969) noted no such response in the toads, *Bufo boreas* and *B. marinus*. In this report the effects of diurnal injections of ovine prolactin on fattening in two euryhaline cyprinodontid fishes, *Cyprinodon variegatus* and *Fundulus similis* are examined.

MATERIALS AND METHODS

Both *Cyprinodon variegatus* and *Fundulus similis* were obtained by seining in Corpus Christi Pass near Port Aransas, Texas in early September. A sample of each species were sacrificed immediately to determine the initial level of lipid (Tables 1 and 2); this sample will hereafter be referred to as the initial controls. Sexually mature fish used for experimental purposes were placed in plastic aquaria (18 l) supplied with aerated sea water (10 fish/aquarium). Experimental fish were allowed to acclimate to laboratory conditions for four days prior to experimental treatment. Animals were exposed to temperatures which varied between 17.5° and 19.5°C and a 13 hr light, 11 hr dark (13L/11D) photoperiod. Fish were fed *ad libitum* twice daily, after each injection period, on a commercial fish food (Tetra-Min).

All *Cyprinodon* used in these experiments weighed between 2.00 and 3.50 g, and all *Fundulus* between 3.00 and 5.00 g. Both male and female fish were used. Animals of each species were

divided into four groups which served as early and late injection groups and their respective controls. The experimental groups received a total of seven 0.5 IU/fish injections (daily) of ovine prolactin (Mann Research Laboratory) or the vehicle, marine teleost ringer solution (Nicoll and Bern, 1964). Intraperitoneal injections (0.1 cc) of hormone or vehicle were made two hrs after the onset of the photoperiod or eight hrs after the onset of the light period.

Twenty-four hrs after the last injection, fish were killed by severing the spinal cord. Following removal of the gonads, fish were weighed and placed in a vacuum oven (65°C) for dessication. Dried carcasses were weighed and lipids extracted in a solution of chloroform, ether and methanol (1:1:1) for 12 days. Following the extraction and another drying period, the carcasses were again weighed. The difference in the two dry weights was taken to be body lipids. Differences in lipid indices between groups were tested by Student's "t" test.

RESULTS

The time that prolactin was injected during the photoperiod markedly affected the influence of this hormone on lipid stores in both *Cyprinodon* and *Fundulus*. In the *Cyprinodon* receiving early prolactin injections both the dry lipid index (mg lipid/g dry body weight) and the wet lipid index (mg lipid/g wet body weight) decreased significantly ($P<0.01$) compared to the saline injected controls and the initial controls (Table 1). Compared to the initial controls, the dry lipid index of fish receiving early prolactin injections decreased 33%, whereas lipid in the saline injected controls increased 5%. In *Fundulus* receiving early prolactin injections the dry and wet lipid indices were significantly less ($P<0.001$) than those of the saline controls (Table 2); these indices were also significantly lower ($P<0.001$) than those of the initial controls. Although lipid content of the *Fundulus* saline controls decreased compared to the initial controls (Table 2), the lipid fraction of the fish receiving early prolactin injections decreased even more, by approximately 85%.

Late injection of prolactin increased significantly ($P<0.001$) both the dry and wet lipid indices of *Cyprinodon* compared to the saline injected and initial controls (Table 1); the dry lipid index increased 89% and the wet lipid index increased 96% in this prolactin group. In *Fundulus* given late injections of prolactin, both lipid indices were significantly greater ($P<0.001$) than those of the saline controls (Table 2). Lipid content of the saline controls decreased from initial levels (by 62–66%), but prolactin injections late in the photoperiod essentially maintained fish at the initial level of fatness.

Neither prolactin nor saline injections significantly influenced the body water in these two species (Tables 1 and 2).

DISCUSSION

Ovine prolactin had a marked effect on lipid metabolsim of both *Cyprinodon variegatus* and *Fundulus similis* when these fish were held on a long (13L/11D) photoperiod. These results are similar to those reported by Lee and Meier (1967) and Meier (1969) in *Fundulus chrysotus* and Mehrle and Fleming (1970) in *Fundulus kansae*. Moreover, in all of these cyprinodontid fishes ovine prolactin promotes fattening if injections are given eight hours after the beginning of the photoperiod, but induces lipid catabolism when the hormone is given two hours

TABLE 1

Changes in lipid reserves in *Cyprinodon variegatus* following diurnal injections of ovine prolactin

	n	Percent water ($\bar{X}\pm$S.E.)	LIPID mg/g dry wt. ($\bar{X}\pm$S.E.)	LIPID Percent change*	LIPID mg/g wet wt. ($\bar{X}\pm$S.E.)	LIPID Percent change*
Initial controls	10	73.1 ± 0.5	123 ± 7	. .	32.2 ± 1.6	. .
Early saline injected	8	73.9 ± 0.1	146 ± 8	+5%	38.2 ± 2.6	+15%
Early prolactin injected	12	71.8 ± 0.3	83 ± 6	−33%	23.4 ± 5.4	−27%
Late saline injected	8	74.7 ± 0.4	144 ± 11	+5%	33.2 ± 2.9	+3%
Late prolactin injected	10	72.9 ± 0.4	233 ± 9	+89%	63.0 ± 3.6	+96%

* Change in lipid index compared to initial controls.

TABLE 2

Changes in lipid reserves in *Fundulus similis* following diurnal injections of ovin prolactin

	n	Percent water ($\bar{X}\pm$S.E.)	LIPID mg/g dry wt. ($\bar{X}\pm$S.E.)	LIPID Percent change*	LIPID mg/g wet wt. ($\bar{X}\pm$S.E.)	LIPID Percent change*
Initial controls	10	71.8 ± 0.4	164 ± 7	. .	46.8 ± 2.0	. .
Early saline injected	8	74.5 ± 0.5	57 ± 8	−68%	15.1 ± 2.0	−72%
Early prolactin injected	10	73.7 ± 0.4	25 ± 4	−85%	6.5 ± 1.0	−86%
Late saline injected	8	74.2 ± 0.3	63 ± 3	−62%	16.0 ± 0.7	−66%
Late prolactin injected	11	74.7 ± 0.2	170 ± 10	+4%	43.5 ± 3.3	−7%

* Change in lipid index compared to initial controls.

after the beginning of the light period. Thus, the cirdadian rhythm in the lipogenic response to prolactin appears to be general throughout the cyprinodontids. Whether other families of fishes show similar responses is presently unknown.

Under the laboratory conditions employed here, saline injected controls of *Cyprinodon* fattened whereas the saline controls of *Fundulus* became more lean (see Tables 1 and 2). Whether this difference in lipid metabolism in the two species was a consequence of laboratory conditions or whether it reflects seasonal differences in metabolism cannot be presently explained. It can be said that both species fed voraciously during the course of these experiments. Whatever the cause of the differences, thsese results suggest that caution should be used in comparing the effects of specific treatments on different species, even under identical laboratory conditions.

The diurnal variation in the lipogenic response to prolactin remains somewhat of an enigma. Meier (1970) showed that phasing of the rhythm of response to prolactin in *Fundulus chrysotus* could be obtained by injections of thyroxine; he suggested then, that the regulation of fat stores involves a synergistic relationship between these two hormones. Recently, however (Meier, *et al.*, 1971a, b), it was suggested that temporal synergisms of adrenal steroids and prolactin control fat levels in four classes of vertebrates. Caution must, nonetheless, be used in interpreting these results since Mehrle and Fleming (1970) showed that

hypophysectomized *Fundulus kansae* respond similarly to intact fish with regard to diurnal prolactin treatment. Further investigatison is required to define more precisely the interaction of prolactin, the interrenal and the thyroid in lipid metabolism.

Whether fish prolactin functions in lipid metabolism or whether ovine prolactin mimics some other fish hormone is also equivocal. Experiments with growth hormone, ACTH and TSH might help elucidate this problem. Indeed, mammalian prolactin has been shown to stimulate the interrenal of some teleosts (Chambolle, 1967a, b; Ball and Fleming, unpublished cited in Ball and Ensor, 1969) and also the thyroid (Olivereau, 1966). Mammalian luteinizing hormone (LH) also has a lipogenic effect in fish (Lee and Meier, 1967). LH, however, has been shown to stimulate the fish interrenal (Sundararaj and Goswami, 1967). Thus, it remains to be determined whether prolactin influences lipid metabolism directly or via other endocrine glands. Nonetheless, our results lend further credence to Meier's suggestion that "physiological time" must be considered in endocrine experiments.

ACKNOWLEDGMENTS

This work was supported by NSF grant GB 22995.

LITERATURE CITED

BALL, J. N. and D. M. ENSOR. 1969. Aspects of the action of prolactin on the sodium metabolism in cyprinodont fishes. In "La Specificité zoologique des hormones hypophysaires et de leurs activities." *Colloques int. Cent. natn. Rech. Scient.* **177:** 215–224.

CHAMBOLLE, P. 1967a. Influence de l'injection d'A.C.T.H. sur la survie de *Gambusia sp.* (Poisson Téléostéen) privé d'hypophyse. *C. r. hebd. Séanc. Acad. Sci., Paris.* **264:** 1464–1466.

————. 1967b. Evolution de l'organe interrénal chez la femelle de *Gambusia sp.* (Poisson Téléostéen). *C. r. hebd. Séanc. Acad. Sci., Paris.* **265:** 1514–1517.

LEE, R. W. and A. H. MEIER. 1967. Diurnal variations of the fattening response to prolactin in the golden top minnow, *Fundulus chrysotus. J. exp. Zool.* **166:** 307–315.

MEHRLE, P. M. and W. R. FLEMING. 1970. The effect of early and midday prolactin injection of the lipid content of *Fundulus kansae* held on a constant photoperiod. *Comp. Biochem. Physiol.* **36:** 597–603.

MEIER, A. H. 1969. Diurnal variation of metabolic responses to prolactin in lower vertebrates. *Gen. comp. Endocr.*, Suppl. **2:** 55–62.

————. 1970. Thyroxin phases the circadian fattening response to prolactin. *Proc. Soc. exp. Biol Med.* **133:** 1113–1116.

———— and K. B. DAVIS. 1967. Diurnal variations of the fattening response to prolactin in the white-throated sparrow, *Zonotrichia albicollis. Gen. comp. Endocr.* **8:** 110–114.

————, T. N. TROBEC, M. M. JOSEPH and T. M. JOHN. 1971a. Temporal synergism of prolactin and adrenal steroids in the regulation of fat stores. *Proc. Soc. exp. Biol Med.* **137:** 408–415.

———— and D. D. MARTIN. 1971b. Temporal synergism of corticosterone and prolactin controlling fat storage in the white-throated sparrow, *Zonotrichia albicollis. Gen. comp. Endocr.* **4:** 457–471.

OLIVEREAU, M. 1966. Action de la prolactine chez l'Anguille intact et hypophysectomisée. I. Système hypophysothyroïdien et pigmentation. *Gen. comp. Endocr.* **6:** 130–143.

SUNDARARAJ, B. I. and S. V. GOSWAMI. 1967. Effect of metopiron (SU-4885) on luteinizing hormone and corticosteroid-induced ovulation and spawning in hypophysectomized catfish, *Heteropneustes fossilis* (Bloch). *J. exp. Zool.* **163:** 49–54.

ZIPSER, R. D., P. LICHT and H. A. BERN. 1969. Comparative effects of mammalian prolactin and growth hormone on growth in the toads *Bufo boreas* and *Bufo mirinus*. *Gen. comp. Endocr.* **13:** 382–391.

SPRAY-MARKING JUVENILE SHRIMP WITH GRANULAR FLUORESCENT PIGMENT

Robert C. Benton and Donald Lightner

Fishery Biologists, National Marine Fisheries Service Biological Laboratory Galveston, Texas 77550

Contribution No. 323 from the National Marine Fisheries Service Biological Laboratory, Galveston, Texas 77550

ABSTRACT

Spray-marking with fluorescent pigment was tested experimentally in the laboratory as a marking method for juvenile (40 to 80 mm total length) penaeid shrimp. Granular fluorescent pigment marked juvenile shrimp satisfactorily when sprayed at pressures above 150 psi at a distance of 12 inches. Mark retention was best in 80-mm juvenile shrimp spray-marked at a pressure of 240 psi. Mortality directly attributable to spray-marking was negligible.

INTRODUCTION

Studies on the dynamics and distribution of shrimp populations typically require the use of marked shrimp. The usual methods of marking shrimp such as tagging with internal and external tags and staining by injection of dyes require handling each shrimp individually (Neal, 1969), which limits the numbers of shrimp that can be marked successfully. The small size of juvenile penaeid shrimp (25 to 110 mm total length, i.e., tip of telson to tip of rostrum) and the necessity of handling each shrimp individually during marking limits the usefulness of these techniques for marking large numbers of juvenile shrimp.

Jackson (1959) originally introduced the fluorescent pigment spray-mark as a rapid, inexpensive method of mass-marking large numbers of fish with a minimum amount of handling and injury to the fish. More recent work using this technique has added improvements and refinements of spray pressures and granular pigment sizes for use with various sizes and species of fish (Phinney, Miller and Dahlberg, 1967; Phinney and Mathews, 1969; Hennick and Tyler, 1970).

K. K. Chew (personal communication, University of Washington, Seattle, Washington) used fluorescent pigment granules to spray-mark spot shrimp (*Pandalus* sp.), but found that the dye material dissipated even before the shrimp had molted. R. Butler and A. N. Yates (personal communication, Biological Station, Nanaimo, B.C.) successfully marked spot shrimp with sprayed fluorescent pigment and reported mark retention of about a month.

Spray-marking with granular fluorescent pigment in the present study was examined as a potential marking method for juvenile penaeid shrimp.

MATERIALS AND METHODS

The techniques used in the present study were modifications of those used by Jackson (1959) and Phinney (1966). Tracer-Glo[1] No. 500-A14 orange granular fluorescent pigment (Wildlife Supply Co., Saginaw, Michigan) of 50 to 60 grit size was sprayed on juvenile white (*Penaeus setiferus*) and brown (*P. aztecus*) shrimp using an air blast gun especially designed for use with Tracer-Glo pigments. Shrimp were sprayed from a distance of 12 inches (30.5 cm) at pressures of 80, 100, 120, 150, 180, 220, and 240 pounds per square inch (psi) and returned to the water immediately after being spray-marked.

Marked and unmarked shrimp were held in identical 500-liter fiberglass tanks. Experimental and control groups were examined daily for mortalities and dead shrimp were removed. Water temperature was monitored but not controlled. At 4-day intervals the marked shrimp were examined for mark retention using ultraviolet light in a darkened room.

Shrimp used in this study ranged in average size from 50 to 80 mm total length and were obtained from the Galveston Bay area.

TABLE 1

Percent retention of fluorescent spray-mark in juvenile penaeid shrimp averaging 80 mm total length in relation to time and spray pressure

Number of days after spray-marking	Spray pressure (in pounds per square inch)						
	80	100	120	150	180	220	240
	Percent						
4	0	0	0	88.8	87.8	77.0	100
8	—	—	—	83.3	85.4	60.7	100
12	—	—	—	83.3	60.0	59.2	100
16	—	—	—	83.3	57.7	57.6	100
20	—	—	—	80.5	56.8	50.0	100
70	—	—	—	—	—	—	100
Number marked	50	51	55	48	79	75	63

— = No observation made.

RESULTS

Pigment granules in spray-marked shrimp (visible as spots of orange fluorescence under ultraviolet light) were primarily located in or under the exoskeleton of the abdominal segments and in the paired appendages (Fig. 1). The tougher exoskeleton of the carapace usually was not penetrated by pigment granules and typically showed no fluorescence.

Spray pressures of 80, 100, and 120 psi were found to be too low for marking juvenile shrimp. None of the shrimp spray-marked at these pressures retained pigment longer than 4 days. Satisfactory retention of the mark for the 20-day period of the experiment was obtained using air pressures of 150 to 240 psi. Retention in 80-mm shrimp spray-marked at 180 and 220 psi was lower (Table 1) than those marked at 150 psi and 240 psi.

Water temperature differences during these experiments may account for these apparent discrepancies. The average water temperature during the 150 psi marking experiment was 15°C, while that for experiments run at 180, 220,

[1] Trade names referred to in this publication do not imply endorsement of commercial products.

FIG. 1. Photograph (using ultraviolet light) of spray-marked juvenile brown shrimp (*Penaeus aztecus*) 4 days after being marked. Fluorescent pigment granules visible as bright spots are located primarily in the abdominal region and on the appendages.

and 240 psi averaged about 22°C. The lower temperature in the 150 psi experiment may have masked the effect of molting on mark retention. Molting may have been a factor at the higher temperature in the experiments run at 180 and 220 psi. However, 97% of the 80-mm shrimp spray-marked at 240 psi and held at 21°C molted during the 20-day experiment, yet none lost the mark during this

period. Fluorescent pigment granules apparently lodged in tissues beneath the exoskeleton in these shrimp, decreasing or eliminating the probable effect of molting on mark retention. Some of these shrimp were held for an additional 50 days. All 11 shrimp (80 mm) surviving 70 days after spray-marking at 240 psi had retained the mark.

Retention of the spray-mark in shrimp increased with increased average length of shrimp (Fig. 2). One-hundred percent of juvenile shrimp averaging 80 mm in

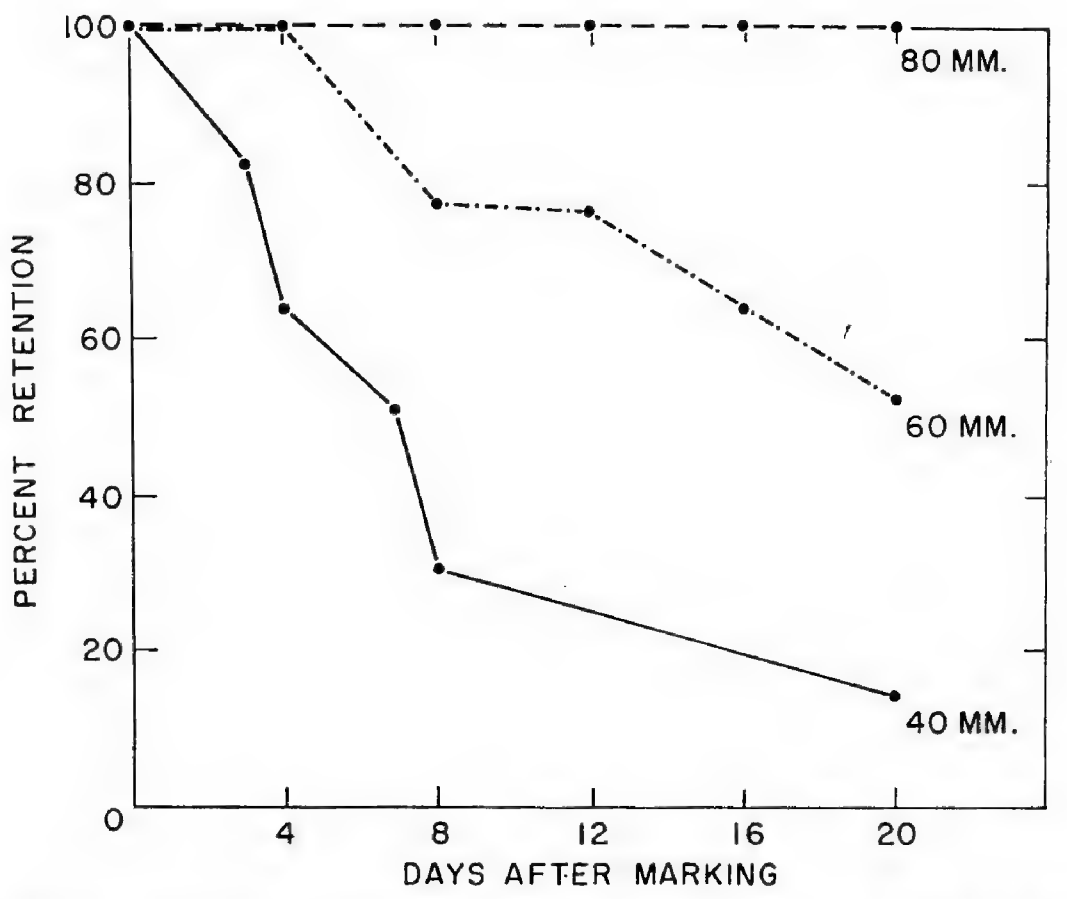

FIG. 2. Percent retention of mark in juvenile penaeid shrimp of three size groups spray-marked with granular fluorescent pigment at a pressure of 240 psi.

TABLE 2

Percent retention of fluorescent spray-mark in juvenile penaeid shrimp in relation to size and time after spray-marking at 240 psi

Number of days after spray-marking	Average length (in millimeters)		
	40	60	80
	Percent		
3	82.5	—	—
4	64.3	100	100
7	51.1	—	—
8	30.6	77.5	100
12	—	76.3	100
16	—	64.2	100
20	14.8	52.2	100
70	—	—	100
Number marked	125	222	63

— = No observation made.

total length retained pigment 20 days after being spray-marked at 240 psi, while shrimp averaging 60 mm and 40 mm in total length had only 52.2% and 14.8% mark retention after 20 days, respectively, when spray-marked at the same pressure (Table 2).

Mortality resulting directly from spray-marking was negligible (always less than 5%) in the experiments reported here, with only an occasional mortality occurring within the first 24 hours after spray-marking. Holding mortalities in control and marked groups were high, however, and necessitated termination of formal experiments after 20 days. These mortalities were primarily due to cannibalism.

LITERATURE CITED

HENNICK, DANIEL P. and RICHARD W. TYLER. 1970. Experimental marking of emergent pink salmon (*Oncorhynchus gorbuscha*) fry with sprayed fluorescent pigment. *Trans. Am. Fish. Soc.* **99**(2): 397–400.

JACKSON, C. F. 1959. A technique for mass-marking fish by means of compressed air. *Tech. Circ. New Hamps. Fish Game.* **17**: 8 pp.

NEAL, RICHARD A. 1969. Methods of marking shrimp. *Fish. Rep. FAO No.* 57, Vol. **3**, pp. 1149–1165.

PHINNEY, DUANE E. 1966. Mass-marking small fish with fluorescent pigment by means of compressed air. *Univ. Washington Fish. Res. Inst. Circ.* **66**(6): 4 p.

PHINNEY, DUANE E., DENNY M. MILLER and MICHAEL L. DAHLBERG. 1967. Mass-marking young salmonids with fluorescent pigments. *Trans. Am. Fish. Soc.* **96**: (2): 157–162.

PHINNEY, DUANE E. and STEPHEN B. MATTHEWS. 1969. Field tests of fluorescent pigment marking and finclipping of coho salmon. *J. Fish. Res. Bd Can.* **26**(6): 1619–1624.

GROWTH AND SEASONAL DISTRIBUTION OF THE ELASMOBRANCH *DASYATIS SABINA*

M. Sage, R. G. Jackson, W. L. Klesch and V. L. deVlaming

University of Texas Marine Science Institute at Port Aransas

ABSTRACT

Young of the stingray *Dasyatis sabina* along the Texas Gulf Coast were born in summer of 1971 at a weight of 50 g. Weight frequency histograms indicate that the growth of females in their first year is approximately 200 g. In their second year when females start to reproduce they show an apparent increased growth rate only part of which is accounted for by the weight of the developing embryos. Thereafter growth continues at the same rate as in first year animals. Males grow at a slower rate of 150 g a year; the weights of some large individuals indicate an age of at least 6 years. The seasonal distribution of *Dasyatis* is discussed.

INTRODUCTION

The stingray *Dasyatis sabina* is one of the comonest vertebrates encountered when trawling along the Texas coast. Although edible this stingray is not marketed and there is a consequent lack of information available on its life history. Gunter (1945) concluded that *Dasyatis* may breed from the spring to the fall; the onset of low temperatures in the fall result in a movement of animals from the bays into the Gulf, although salinity changes appeared not to be important in determining the distribution of these animals (Gunter, 1945). In this laboratory *Dasyatis* is used in physiological studies and as a consequence large numbers are caught throughou the year enabling construction of size-frequency distribution histograms from which normal growth rates can be determined. The present data indicates that growth of *Dasyatis* differs from that previously described for another batoid, *Raia clavata* (Steven, 1936).

MATERIALS AND METHODS

Dasyatis sabina (Le Sueur) were collected in a trawl similar to those used for shrimp on the Gulf coast. The trawl was modified by the removal of half the rings constricting the neck. This modification reduces the bruising of animals. Over 300 animals were collected throughout a twelve-month period ending September 1971. Collections yere made both in the shallow bays where the animals may be found from late spring to fall, and in the inshore waters of the Gulf of Mexico, where they congregate in the winter.

RESULTS

Growth

The weight-frequency histograms for male and female animals collected in the six-month periods of September to February and March to August are seen

in Figure 1. The alternating frequency modes for the two six month periods indicate that each mode represents a one year age class. From this it can be seen that males grow at approximately 150 g per year. Females grow 200 g in their first year followed by a marked increase in their second year. Presumably this represents growth of embryos as well as maternal growth. Growth of females in subsequent years is similar to the first year rate of 200 g per year. From these growth rates it seems likely that the largest animals caught were at least 6 years old. Females containing mature embryos were only recorded in June and July of 1971. Young born in captivity had a weight of 50 g while the smallest caught in the wild weighed slightly less (48 g).

Observations on the Distribution of Dasyatis *in the Bays and Gulf of Mexico*

The distribution of *Dasyatis* varies with the season. The animals move into the Gulf for the winter and into the bays for the summer. In the bays the adult females and new born young move to very shallow water where they are observed, but are inaccessible to the trawl. In the late fall adults and juveniles were caught in two separate but neighboring locations in the Gulf. The move-

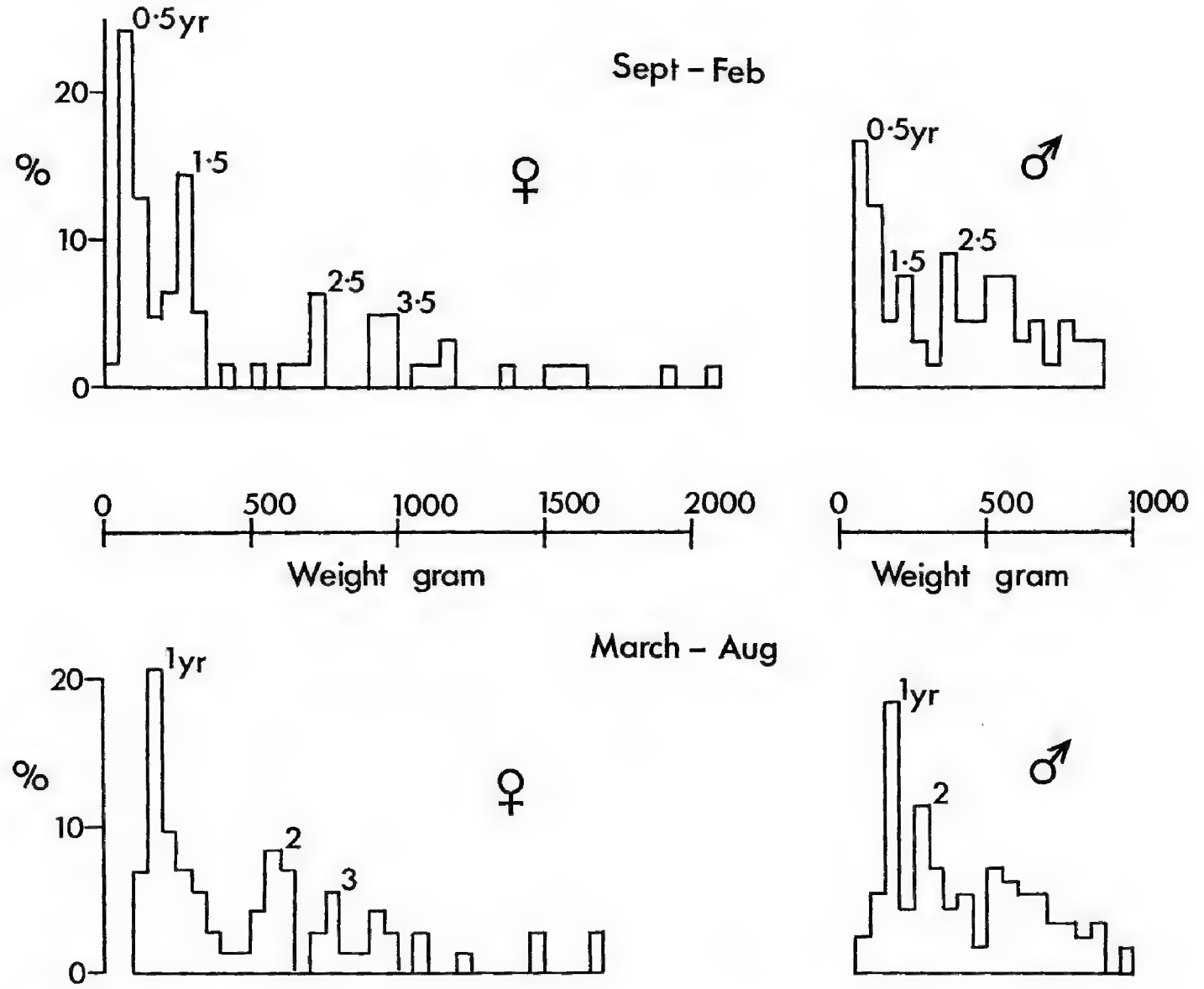

FIG. 1. Frequency-weight distribution curves for the six month periods September to February and March to August for male and female *Dasyatis sabina*. The probable ages of the animals comprising the more clearly identifiable modes are indicated.

ment to the Gulf follows a drop in bay temperature; thus these animals are caught in the fall in the tide trap in the channel between the bays and the Gulf at Port Aransas following cold northerly winds. Although *Dasyatis* are known to enter fresh water (Gunter, 1938), a drop in salinity may also stimulate movement into the Gulf. Following tropical storm Fern in September 1971 the salinity of the water in the Pass at Port Aransas dropped to 4.5 ppt and a large number of rays moved out from the bays and were caught in trawls in the shallow Gulf. In winter no young of less than one year old were caught, an observation also made by Gunter (1945); they may be farther off shore. In February to March there is an increase in density of adult animals in the inshore waters of the Gulf. These inshore aggregations may be for copulation although there is no direct evidence for this. These inshore aggregations have a population density of at least ten times that of any other time of the year (as judged by numbers caught per unit trawling time).

DISCUSSION

A consequence of the varying distribution of different aged animals at different times of the year is that the collection of *Dasyatis* reported here are not random samples of the population. As a result, nothing can be determined from these data about mortality rates. The sharpness of the frequency peaks for each age size group indicates that Gunter's (1945) suggestion for a long breeding season for this species may be incorrect. In 1971 pregnant females were only found until July. The data can and have been used to estimate growth rates which differ for males and females. The biological advantage for such a difference could be that females, which provide nutrients for the developing embryos, rapidly attain a size capable of fulfilling these functions while males, which supply only sperm need no special size. Differences in the growth rates of males and females have also been observed in *Squalus acanthias* (Holden and Meadows, 1962) although other investigators have failed to observe such differences in either rays (Steven, 1936) or sharks (Olson, 1954).

The present observations on the movement of animals between the bays and the Gulf indicate that a rapid drop in salinity such as followed tropical storm Fern may also be a factor in initiating movement of animals from the bays to the Gulf, in addition to the previously known factor of lower temperatures.

ACKNOWLEDGMENTS

We are indebted to Mr. John Thompson and his staff at the Marine Science Institute especially the boat captains E. Wingfield and J. Shanklin for help in collecting stingrays. This work was supported by NSF grant GB 22995.

LITERATURE CITED

GUNTER, G. 1938. Notes on the invasion of fresh water by fishes of the Gulf of Mexico, with special reference to the Mississippi River system. *Copeia* **1938**(2): 69–72.

GUNTER, G. 1945. Studies on marine fishes of Texas. *Publs. Inst. mar. Sci. Univ. of Tex.* **1**: 1–190.

HOLDEN, M. J. and MEADOWS, P. S. 1962. The structure of the spine of the spur dogfish Squalus acanthias L. and its use for age determinations. *J. mar. biol. Ass. U.K.* **42**: 179–197.

OLSON, A. M. 1954. The biology migration and growth rate of the school shark *Galeorhinus australis* (Macleay) (Carcharhanidae) in Southeastern Australian waters. *Aust. J. mar. Freshwater Research.* **105**: 353–410.

STEVEN, G. A. 1936. Migrations and growth of the thornback ray *Raia clavata J. mar. biol. Ass. U.K.* **20**: 605–614.

NOTES ON DISTRIBUTION, SIZE, AND OVARIAN DEVELOPMENT OF SOME PENAEID SHRIMPS IN THE NORTHWESTERN GULF OF MEXICO, 1961–62[1]

Harold A Brusher, William C. Renfro,[2] and Richard A. Neal

Fishery Biologists, National Marine Fisheries Service Biological Laboratory
Galveston, Texas 77550

ABSTRACT

Between January 1961 and December 1962, shrimp were taken monthly using commercial shrimping gear at a series of offshore stations in the northwestern Gulf of Mexico. The general distribution of nine species not presently utilized commercially was determined. The relative abundance of these shrimp in various depths and areas are noted. General seasonal changes in catch per hour were reported for the more abundant species, and size distributions for each species were presented. Examination of ovaries revealed "ripe" females in nearly every month at all depths occupied by a species. Seasonal increases in the percentages of ripe females were noted for some species. As a result of these collections the recorded range of *S. atlantidis* was extended westward into the northwestern Gulf of Mexico.

INTRODUCTION

To gain better understanding of the distribution and biology of penaeid shrimp in the northwestern Gulf of Mexico, a field survey was conducted from January 1961 to December 1962. During this survey, nine species not extensively utilized commercially were taken in trawl samples in addition to commercially important species. The non-utilized species were: *Sicyonia brevirostris* Stimpson, *Sicyonia dorsalis* Kingsley, *Sicyonia stimpsoni* Bouvier, *Trachypenaeus similis* (Smith), *Trachypenaeus constrictus* (Stimpson), *Solenocera vioscai* Burkenroad, *Solenocera atlantidis* Burkenroad, *Xiphopenaeus kroyeri* (Heller) and *Parapenaeus longirostris* (Lucas). This report contains information concerning their distribution, size and ovarian development during the 2-year period.

PROCEDURES

Sampling station locations during the survey are shown in Figure 1. Stations were established so that sampling would be conducted in areas and depths (14 to 110 m) representative of off-

[1] Contribution No. 328, National Marine Fisheries Service Biological Laboratory, Galveston, Texas 77550.

[2] Present address: International Atomic Energy Agency Laboratory of Marine Radioactivity, Musee Oceanographique, Monaco.

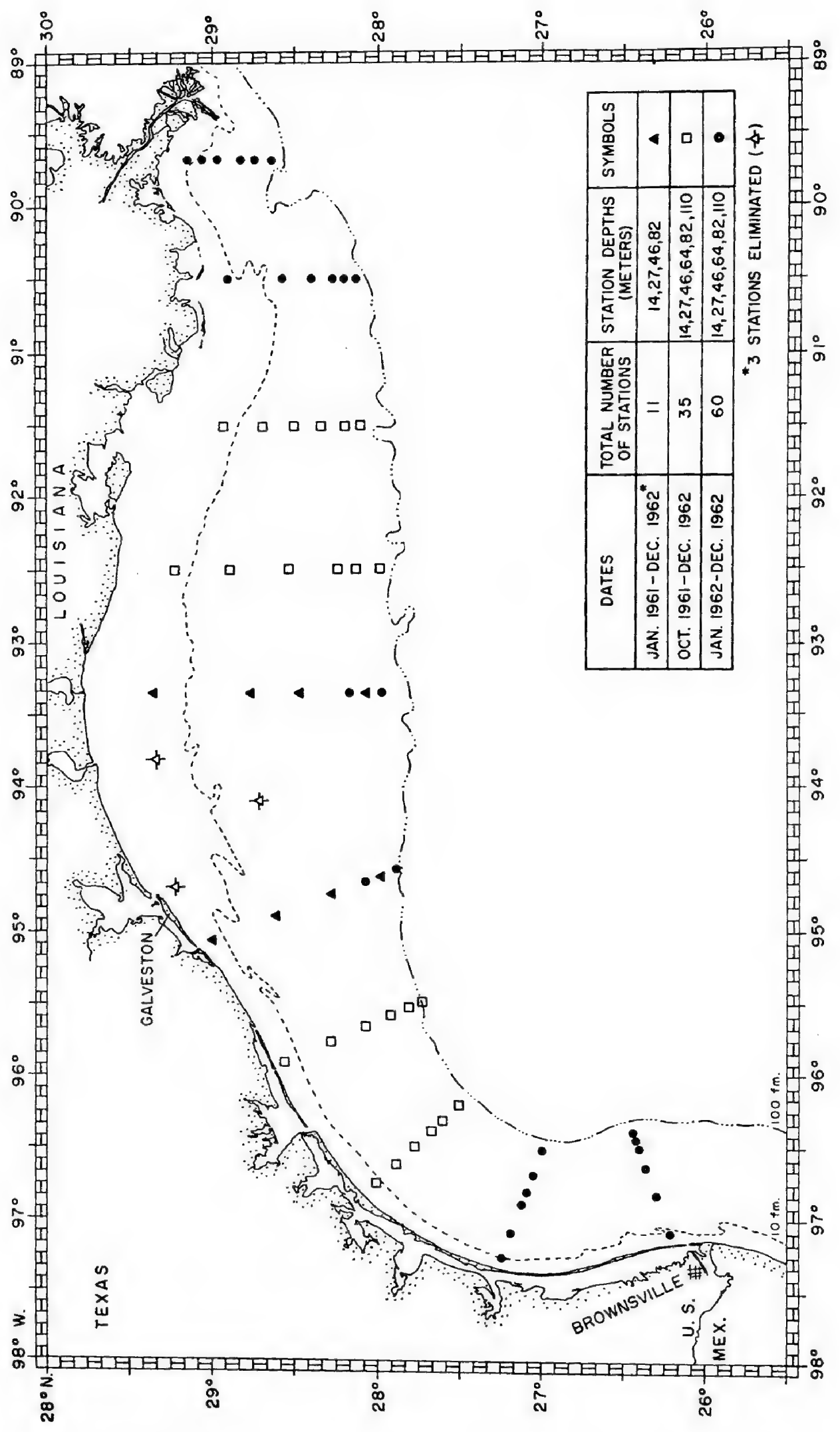

FIG. 1. Station locations at which shrimp were collected in 1961 and 1962.

shore shrimp habitat. Trawling was done from commercial shrimp-fishing vessels using 13.7-m flat trawls with 5.1-cm stretched mesh. The trawl was towed for 1 hour at each station. Cruises were made every 3 to 4 weeks, and collections were made upon arrival at a station regardless of time of day.

If fewer than 50 specimens of *S. brevirostris* or fewer than 25 of any other penaeid species were taken at each station, sexes and total lengths (tip of rostrum to tip of telson) were recorded for all specimens. If larger numbers were taken, sexes and total lengths were recorded for a minimum of 50 *S. brevirostris* and 25 of each of the other species. Sex was determined by examining the external reproductive organs. Portions of ovaries from the females that were measured were fixed in Bouin's solution which was replaced with 50% alcohol after 24 hours. In the laboratory the tissues were dehydrated in alcohol, embedded in paraffin, sectioned in thicknesses of 10 to 15 μ, and stained differentially with hematoxylin and eosin.

The developmental stages of ovaries reported by King (1948) were used to describe the histological condition of ovaries examined. The proportion of females in the ripe stage was used as an index of spawning activity. Based on King's description, the ripe stage is characterized by the presence of prominent rodlike bodies embedded in the egg cytoplasm, the size and shape of the ovary, and the acidophilic nature of the cytoplasm.

ANALYSIS

To facilitate analysis, data are grouped in several different ways. Average catches in individuals per hour of each species are presented by station number in Table 1. Because sampling was done both at night and during the day, all catches were used to describe bathymetric distribution (Table 2). Some indication of the differences in average catches between day and night, however, can be seen in Table 3 in which day and night catches are summarized. Monthly catches (Table 4) are presented only for the four most abundant species and because each of these is more vulnerable to the fishing gear during the night than during the day, only night catches are used as indices of seasonal abundance.

Although the sampling procedure used was not adequate to provide detailed information on bathymetric distributions, it permitted rough estimates of relative abundance at different sampling depths. In addition, the mesh size of the otter trawls used were designed for the capture of larger, commercially important shrimp. Thus, the actual abundances of the smaller less vulnerable species (i.e. shrimp less than 80 mm total length) are probably not accurately represented.

Length frequency distributions of the five most abundant species are illustrated in Figure 2 and those for the least abundant species are presented in Table 5. These data represent catches from all months and depths. Although evident, it should be mentioned that *S. brevirostris*, *S. dorsalis* and *X. kroyeri*, represent narrow sexula dimorphism. On the other hand, *Trachypenaeus sp.*, *S. vioscai* and *P. longirostris* appeared to exhibit wide sexual dimorphism with respect to size.

The data on development stages of ovaries were inadequate to show actual spawning seasons, but as indicated by the percentages of ripe females found each month, the portions of the females which were ready to spawn changed periodically (Table 6).

RESULTS

In the sections which follow, information derived during this survey is presented for each species. The order of discussion is based on total numbers caught as follows: *S. brevirostris*—32,218, *S. dorsalis*—17,674, *T. similis*—12,858, *S.*

TABLE 1

Average catch (individuals per hour) of nine species of penaeid shrimp taken with otter trawls in the northwestern Gulf of Mexico, 1961–62 (Stations 1–31—Texas coast and Stations 32–63—Louisiana coast)

Station number	Depth (meters)	Number of 1-hour trawl hawls	*Sicyonia brevirostris*	*Sicyonia dorsalis*	*Trachypenaeus similis*	*Solenocera vioscai*	*Xiphopenaeus kroyeri*	*Trachypenaeus constrictus*	*Parapenaeus longirostris*	*Solenocera atlantidis*	*Sicyonia stimpsoni*
1	14	13	1.0	0.0	0.6	0.0	2.2	0.2	0.0	0.0	0.0
2	27	12	15.2	72.8	12.8	0.0	0.0	0.0	0.0	0.0	0.0
3	46	12	86.0	5.5	8.1	5.8	0.0	0.0	0.0	0.0	0.1
4	64	10	7.8	0.0	0.5	4.2	0.0	0.0	0.0	0.0	0.0
5	82	9	3.7	0.0	0.0	2.1	0.0	0.1	0.0	0.0	0.0
6	110	8	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0	0.0
7	14	11	1.7	0.0	1.6	0.0	3.9	2.1	0.0	0.0	0.0
8	27	12	0.2	82.3	28.2	0.0	0.0	0.0	0.0	0.0	0.0
9	46	13	0.5	40.0	32.9	4.1	0.0	0.0	0.0	0.0	0.0
10	64	11	0.5	1.6	1.3	4.0	0.0	0.0	0.0	0.0	0.0
11	82	12	4.5	0.0	0.0	10.6	0.0	0.0	0.0	0.0	0.0
12	110	10	0.0	0.0	0.0	10.1	0.0	0.0	0.0	0.0	0.0
13	14	16	0.0	0.1	4.6	0.0	32.4	0.1	0.0	0.0	0.0
14	27	16	0.4	230.9	36.7	0.0	0.1	0.0	0.0	0.0	0.0
15	46	15	1.7	64.8	9.1	24.5	0.0	0.1	0.0	0.0	0.0
16	64	14	1.4	107.1	22.6	22.4	0.0	0.0	0.0	0.0	0.0
17	82	14	6.1	23.2	4.3	10.2	0.0	0.0	0.0	0.0	0.0
18	110	13	0.0	0.0	0.0	5.3	0.0	0.0	0.1	0.0	0.0
19	14	15	0.0	0.5	7.9	0.0	0.3	0.0	0.0	0.0	0.0
20	27	14	7.7	99.9	57.7	0.0	0.0	0.0	0.0	0.0	0.0
21	46	15	40.4	0.4	1.5	0.1	0.0	0.0	0.0	0.0	0.0
22	64	15	69.2	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0
23	82	16	3.7	0.0	0.0	1.8	0.0	0.0	0.0	0.0	0.0
24	110	13	0.0	0.0	0.0	3.4	0.0	0.0	0.2	0.0	0.0

TABLE 1—Continued

Station number	Depth (meters)	Number of 1-hour trawl hawls	*Sicyonia brevirostris*	*Sicyonia dorsalis*	*Trachypenaeus similis*	*Solenocera vioscai*	*Xiphopenaeus kroyeri*	*Trachypenaeus constrictus*	*Parapenaeus longirostris*	*Solenocera atlantidis*	*Sicyonia stimpsoni*
25	14	28	0.1	0.5	36.0	0.0	0.3	0.0	0.0	0.0	0.0
26	27	29	32.1	213.4	70.2	<0.1	0.0	4.9	0.0	0.1	0.0
27	46	29	275.2	0.6	2.2	0.2	0.0	0.2	0.0	<0.1	0.0
28	64	12	5.2	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
29	82	22	2.8	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
30	110	11	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
31	14	17	0.1	0.6	31.6	0.0	8.9	0.0	0.0	0.0	0.0
32	27	18	147.5	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0
33	14	16	7.4	0.6	7.5	0.0	1.1	2.4	0.0	0.0	0.0
34	14	24	33.0	0.2	30.4	0.0	2.0	0.1	0.0	0.0	0.0
35	27	28	359.8	0.0	0.6	0.0	0.0	0.1	0.0	0.2	0.0
36	46	28	105.7	0.2	0.9	0.0	0.0	0.0	0.0	0.0	0.0
37	64	12	26.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
38	82	14	12.3	0.0	0.0	11.9	0.0	0.0	0.0	0.0	0.0
39	110	11	0.0	0.0	0.0	1.4	0.0	0.0	0.1	0.0	0.0
40	14	13	0.1	0.0	14.4	0.0	0.0	0.0	0.0	0.0	0.0
41	27	13	54.6	19.8	79.6	0.0	0.0	0.0	0.0	0.2	0.0
42	46	15	158.9	0.4	1.0	0.3	0.0	0.0	0.0	0.0	0.0
43	64	16	111.7	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
44	82	31	9.5	<0.1	0.0	0.7	0.0	0.0	0.0	0.0	0.0
45	110	12	0.1	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0
46	14	13	0.0	0.0	5.5	0.0	0.0	0.0	0.0	0.0	0.0
47	27	16	2.4	27.1	117.9	0.0	0.0	0.0	0.0	0.0	0.0
48	46	16	9.0	27.2	33.4	45.8	0.0	0.0	0.0	0.0	0.1
49	64	18	11.1	0.4	0.0	2.1	0.0	0.0	0.0	0.0	0.0
50	82	18	0.6	0.0	0.2	0.9	0.0	0.0	0.0	0.0	0.0
51	110	14	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0

TABLE 1—Continued

Station number	Depth (meters)	Number of 1-hour trawl hawls	*Sicyonia brevirostris*	*Sicyonia dorsalis*	*Trachypenaeus similis*	*Solenocera vioscai*	*Xiphopenaeus kroyeri*	*Trachypenaeus constrictus*	*Parapenaeus longirostris*	*Solenocera atlantidis*	*Sicyonia stimpsoni*
52	14	12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
53	27	11	49.4	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0
54	46	13	14.2	0.0	13.0	3.3	0.0	0.0	0.0	0.0	0.0
55	64	14	22.8	0.0	0.3	3.9	0.0	0.0	0.0	0.0	0.0
56	82	14	0.0	0.0	0.0	1.1	0.0	0.0	0.1	0.0	0.0
57	110	12	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
58	14	10	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
59	27	12	0.0	0.0	9.2	0.0	0.1	0.0	0.0	0.0	0.0
60	46	15	0.3	0.3	18.1	7.4	0.0	0.0	0.3	0.0	0.0
61	64	13	0.0	0.0	48.5	66.0	0.0	0.0	5.8	0.0	0.2
62	82	12	0.0	0.0	0.9	14.6	0.0	0.0	1.1	0.0	0.2
63	110	10	0.0	0.0	0.0	7.4	0.0	0.0	0.4	0.0	0.1
Σ	..	951	..	..	..	..	..	..	..	..	..

TABLE 2

Average catch per hour of nine species of penaeid shrimp by depth in offshore waters of Texas and Louisiana, 1961–62

Species	Depth (m) / No. of 1-hour hawls	14 / 98	27 / 100	46 / 84	64 / 62	82 / 72	110 / 54
		Texas coast (longitude 94° 30′ to 97° 30′ W)					
Sicyonia dorsalis		0.3	130.4	19.2	24.7	4.5	0.0
Sicyonia brevirostris		0.3	39.3	113.5	19.4	4.2	0.0
Trachypenaeus similis		17.9	39.7	9.0	5.4	0.9	0.0
Solenocera vioscai		0.0	0.0	6.0	6.5	4.2	4.3
Xiphopenaeus kroyeri		7.7	<0.1	0.0	0.0	0.0	0.0
Trachypenaeus constrictus		0.1	1.6	0.1	0.0	0.0	0.0
Sicyonia stimpsoni		0.0	0.0	<0.1	0.0	<0.1	0.0
Parapenaeus longirostris		0.0	0.0	0.0	0.0	0.0	0.1
Solenocera atlantidis		0.0	<0.1	0.0	0.0	0.0	0.0
	Depth (m) / No. of 1-hour hawls	14 / 87	27 / 79	46 / 89	64 / 63	82 / 98	110 / 62
		Louisiana coast (longitude 89° 30′ to 94° 0′ W)					
Sicyonia brevirostris		10.1	143.3	63.5	40.3	6.4	<0.1
Trachypenaeus similis		13.7	39.6	11.3	10.1	0.1	0.0
Solenocera vioscai		0.0	0.0	10.3	15.6	3.9	2.8
Sicyonia dorsalis		0.2	9.0	4.7	0.0	<0.1	0.0
Parapenaeus longirostris		0.0	0.0	0.1	1.2	0.1	0.1
Xiphopenaeus kroyeri		0.7	<0.1	0.0	0.0	0.0	0.0
Trachypenaeus constrictus		0.5	<0.1	0.0	0.0	0.0	0.0
Sicyonia stimpsoni		0.0	0.0	<0.1	<0.1	<0.1	<0.1
Solenocera atlantidis		0.0	0.1	0.0	0.0	0.0	0.0

TABLE 3

Average catch per hour by day and night for nine species of penaeid shrimp, 1961–62

Species	Night (429 tows)	Day (520 tows)
Sicyonia brevirostris	76.6	6.1
sicyonia dorsalis	33.3	6.5
Trachypenaeus similis	22.6	6.0
Solenocera vioscai	8.5	0.5
Xiphopenaeus kroyeri	0.5	1.1
Trachypenaeus constrictus	0.2	0.3
Parapenaeus longirostris	0.2	<0.1
Solenocera atlantidis	<0.1	<0.1
Sicyonia stimpsoni	<0.1	<0.1

vioscai—3,887, *X. kroyeri*—823, *T. constrictus*—222, *P. longirostris*—103, *S. atlantidis*—12 and *S. stimpsoni*—8.

Sicyonia brevirostris, although not now utilized commercially, may be locally abundant enough to support a small fishery. This species was most abundant in the middle four transects at depths of 27, 46, and 64 m (Tables 1 and 2). Over 90% were taken from seven stations in depths of from 27 to 64 m between longitude 92° and 96° W. Only one individual was caught from 110 m and few were

TABLE 4

Average catch (individuals per hour) of four species of penaeid shrimp by month and depth (based on night tows only)

Month	Depth (m) 14	27	46, 64	82, 110	14	27	46, 64	82, 110
	Sicyonia brevirostris				*Sicyonia dorsalis*			
January	1	43	621	13	1	2	32	0
February	1	23	11	3	0	4	2	0
March	10	23	8	2	1	5	1	0
April	1	13	26	3	1	1	0	0
May	100	60	3	2	1	25	0	0
June	18	234	43	2	1	157	1	0
July	0	509	190	1	0	485	1	0
August	0	495	548	17	0	570	133	0
September	0	159	255	53	0	9	0	0
October	0	139	132	41	0	11	127	154
November	2	15	97	30	0	3	1	1
December	1	83	222	23	1	1	21	0
	Trachypenaeus similis				*Solenocera vioscai*			
January	38	8	10	0	0	0	4	4
February	4	65	21	1	0	0	2	6
March	49	38	24	4	0	0	11	13
April	11	23	3	1	0	0	2	13
May	36	247	7	22	0	0	3	23
June	24	348	82	1	0	0	119	28
July	1	77	10	0	0	0	13	5
August	16	100	8	12	0	0	1	22
September	1	12	1	0	0	0	1	5
October	1	11	3	17	0	0	0	6
November	4	11	5	1	0	0	5	12
December	18	59	1	1	0	0	53	14

collected from depths of 14 or 82 m. Lunz (1957) and Anderson (1956) reported similar bathymetric distributions for *S. brevirostris* off South Carolina. This evidence suggests that this species tends to remain within localized depth zones and coastal areas.

S. brevirostis was more readily captured during darkness than in daylight (Table 3). For this reason, estimates of seasonal abundance were based on night collections only. In Table 4, the mean number of individuals captured in 1-hour night tows indicates that this species reached peak abundance in July and August in depths of 27, 46 and 64 m.

Length-frequency of all *S. brevirostris* measured is presented in Figure 2. Females were, on the average, slightly larger than males. Most individuals measured 80 to 104 mm, suggesting that smaller *S. brevirostris* were not effectively captured by the otter trawls used.

The total numbers of *S. brevirostris* examined for ovary condition are presented in Table 6. Females with "developing" and "yellow" stage ovaries were most

TABLE 5

Length distributions of *T. constrictus*, *P. longirostris*, *S. atlantidis*, *S. stimpsoni* caught during 1961–62

Total length	*T. constrictus*		*P. longirostris*		*S. atlantidis*		*S. stimpsoni*	
	Female	Male	Female	Male	Female	Male	Female	Male
mm				Number				
35–37	–	–	–	–	–	–	3	–
38–40	–	–	–	–	–	–	0	–
41–43	–	–	1	–	1	–	0	–
44–46	–	–	0	–	3	–	0	–
47–49	–	–	0	–	1	–	0	–
50–52	–	–	1	2	3	–	0	–
53–55	–	–	4	2	3	–	2	–
56–58	–	1	3	1	1	–	–	–
59–61	–	3	3	2	1	–	–	–
62–64	2	0	2	–	–	–	–	–
65–67	1	1	4	–	–	–	–	–
68–70	3	2	3	–	–	–	–	–
72–73	6	–	0	–	–	–	–	–
74–76	16	–	3	–	–	–	–	–
77–79	11	–	2	–	–	–	–	–
80–82	10	–	4	–	–	–	–	–
83–85	13	–	4	–	–	–	–	–
86–88	25	–	0	–	–	–	–	–
89–91	8	–	2	–	–	–	–	–
92–94	12	–	0	–	–	–	–	–
95–97	2	–	1	–	–	–	–	–
98–100	2	–	–	–	–	–	–	–
101–103	2	–	–	–	–	–	–	–
104–106	1	–	–	–	–	–	–	–
107–109	1	–	–	–	–	–	–	–

prevalent. However, females having "ripe" eggs were present year-round with highest percentages of ripe ovaries occurring from January through April.

Sicyonia dorsalis is a small rock shrimp taken mainly along the Texas coast at the 27-m stations (Tables 1 and 2). Trawl tows made at night yielded much larger catches than daylight tows (Table 3) and, thus, only night collections are used to indicate seasonal abundance. *S. dorsalis* was present in greatest abundance during July and August (Table 4).

Most *S. dorsalis* caught were 60 to 75 mm long (Fig. 2) and mean lengths differed little between sexes. Females with ripe eggs occurred throughout the year but were present in highest frequency from May through September.

Trachypenaeus similis, a small shrimp most abundant at the 27-m stations (Tables 1 and 2), was caught in smaller numbers in depths of 14, 46, and 64 m, rarely in 82 m and not at all in 110 m. Hildebrand (1954) reported *T. similis* to be second in abundance only to brown shrimp. Most of Hildebrand's collections were from depths of 18 to 44 m. This species was taken in largest numbers in

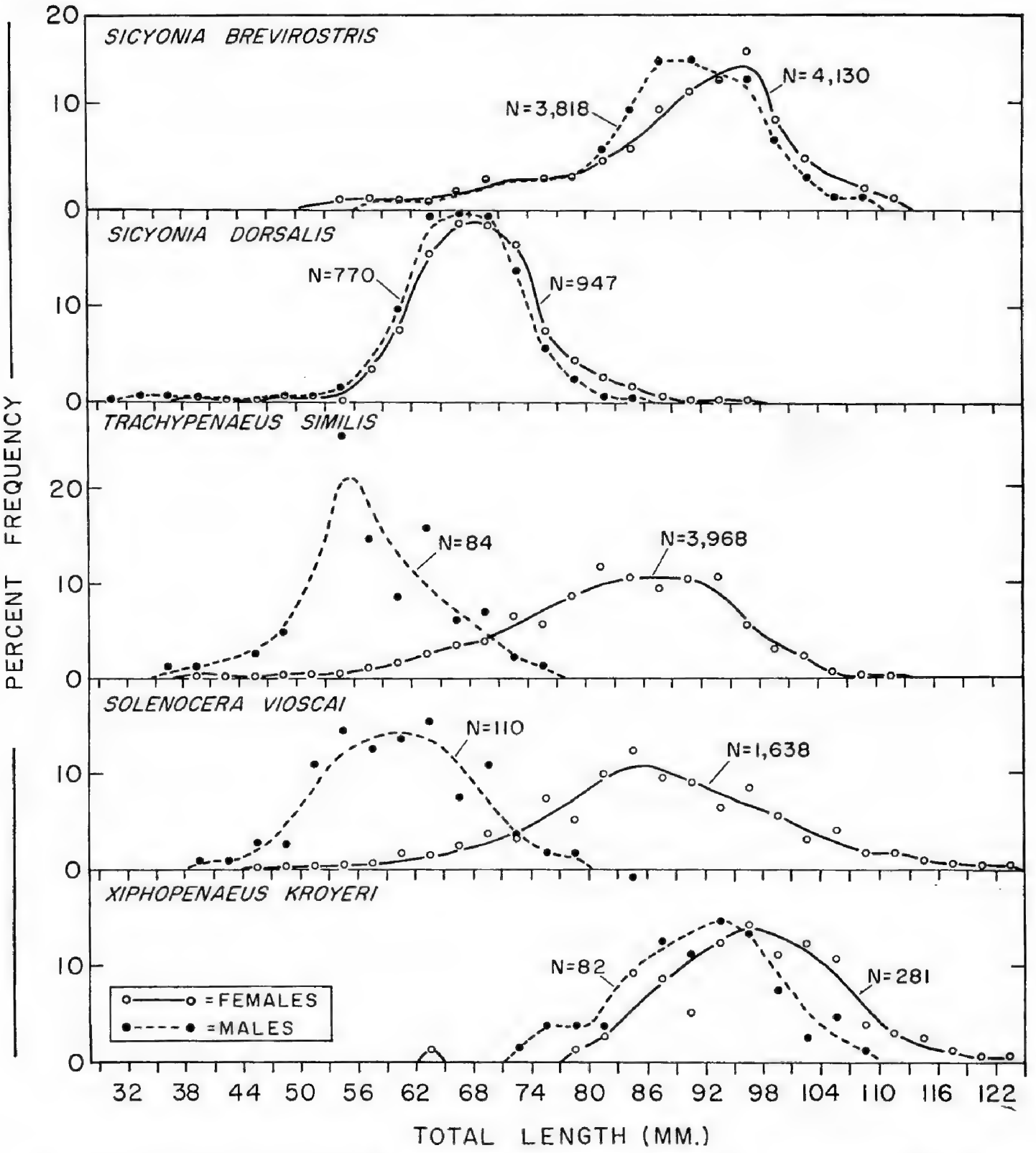

FIG. 2. Length distributions of *S. brevirostris*, *S. dorsalis*, *T. similis*, *S. vioscai* and *X. kroyeri* caught in the northwestern Gulf of Mexico, 1961–62. Curves are fitted by eye.

night trawls (Table 3) and appeared to occur in greatest abundance in May and June.

The differences in size between the sexes was striking. Most females were 70 to 95 mm long whereas the majority of males measured 50 to 70 mm (Fig. 2). Since only about one in every 50 *T. similis* caught were males, most were apparently not large enough to be retained in our nets. Spawning, as indicated by the percent frequency of "ripe" females, appeared to be more intense in June, July and September than in other seasons (Table 6).

Solenocera vioscai, often called "broken back" shrimp by the fishermen, was

TABLE 6

Monthly summary of the percentage of ripe ovaries for four species of penaeid shrimp, 1961–62 (all depths combined)

Month	Species							
	S. brevirostris		*S. dorsalis*		*T. similis*		*S. vioscai*	
	Percent	Number examined	Percent	Number examined	Percent	Number examined	Percent	Number examined
January	15	191	20	20	0	43	4	47
February	22	101	0	11	1	157	14	57
March	17	110	15	13	4	181	12	95
April	25	104	11	9	8	103	6	71
May	9	134	33	30	1	123	5	63
June	7	164	18	73	2	124	12	76
July	8	126	16	56	6	95	13	38
August	13	225	16	89	13	119	10	61
September	8	237	31	74	5	57	10	39
October	9	258	11	68	4	50	7	55
November	17	308	6	17	0	36	14	78
December	7	257	5	19	2	57	6	121
Size range of ripe females	59–113 mm		58–83 mm		59–107 mm		56–107 mm	

never caught in 14- and 27-m depths (Table 1). Instead, this species appeared to be most prevalent at 46- and 64-m stations (Table 2). Based on night tows, which were much more productive than those made in daylight (Table 3), *S. vioscai* was most abundant in June and July. Males have much smaller average lengths than females (Fig. 2) and hence, were probably less vulnerable to the collecting gear used. Females with "ripe" eggs occurred most frequently during the period July-September (Table 6).

Xiphopenaeus kroyeri, commonly called the "seabob," is harvested on a limited commercial basis from Texas to northern Florida. Annual production in our survey area during 1961 and 1962 averaged about 2 million pounds (heads-off weight). This species occurs almost exclusively in near-shore areas, for more than 90% of the commercial catch is reported from depths of 9 m or less. In this survey, only two individuals from a total of 823 were captured in depths greater than 14 m. Almost all the seabobs were taken from September through January along the Texas coast (Tables 1 and 2). *X. kroyeri*, in contrast to previous species, was caught more readily in the daytime (Table 3). Males were apparently slightly shorter than females. Of the few ovaries examined histologically, none were ripe. However, Renfro and Cook (1963) reported gravid seabobs in the vicinity of Galveston from April through October.

Trachypenaeus constrictus is similar in size and superficial appearance to *T. similis*. For this reason, some misidentification of the two species in the field may have occurred. Burkenroad (1934) identified both species in Louisiana and noted that *T. similis* was caught more frequently than *T. constrictus*. Gunter (1950) listed 104 specimens from the vicinity of Aransas Pass as *T. constrictus*

TABLE 7

Station data for *Solenocera atlantidis* caught during 1961 and 1962

Date	Position	Depth in fathoms	Time of day	Number per standard tow
1961				
February 28	28° 40′ N 94° 55′ W	15	Night	3
March 23	28° 45′ N 93° 20′ W	15	Night	6
1962				
May 19	28° 54′ N 92° 30′ W	15	Night	3

with the qualification that some may have been *T. similis*. Hildebrand (1954) recognized only *T. similis* in his study of the brown shrimp grounds in the western Gulf of Mexico. During this survey we recognized *T. constrictus* only infrequently and usually in small numbers.

The small amount of data available from this study suggests that *T. constrictus* inhabits shallow waters (Tables 1 and 2) and may be equally available to day and night trawl tows (Table 3). Only eight individuals were taken at 46 m and one occurred at 82 m. Females had much greater average lengths than males (Table 5). No ripe ovaries were noted among the 49 examined.

Parapenaeus longirostris mainly inhabits the deeper areas in the eastern portion of the survey area (Tables 1 and 2). It was captured almost exclusively at night and females were generally larger than males (Table 5).

Solenocera atlantidis was described by Burkenroad (1939) from a sample of 369 specimens caught in a depth of 35 m and an 8-mm specimen taken by plankton net at a 37-m station off Mississippi. Springer and Bullis (1956) extended its known range eastward to Apalachicola, Florida. The *S. atlantidis* taken during this survey are tabulated in Table 7. These data extend its range westward into the northwestern Gulf of Mexico.

Sicyonia stimpsoni were identified from several collections made during the latter half of 1962. All were females and were caught at night from depths of 46 to 110 m.

LITERATURE CITED

ANDERSON, W. W. 1956. January to April distribution of the common shrimp on the south Atlantic continental shelf. *Spec. Scient. Rept. U.S. Fish Wildl. Serv.* **171**: 1–14.

BURKENROAD, MARTIN D. 1934. The Penaeidae of Louisiana with a discussion of their world relationships. *Bull. Am. Mus. nat. Hist.*, **68**(2): 61–143.

BURKENROAD, MARTIN D. 1939. Further observations on Penaeidae of the northern Gulf of Mexico. *Bull. Bingham Oceanogr. Coll.* **6**(art. 6): 1–62.

GUNTER, GORDON. 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. *Publs Inst. mar. Sci. Univ. Tex.* **1**(2): 7–51.

HILDEBRAND, H. H. 1954. A study of the fauna of the brown shrimp (*Penaeus aztecus* Ives) grounds in the western Gulf of Mexico. *Publs. Inst. mar. Sci. Univ. Tex.* **3**(2): 233–366.

KING, J. E. 1948. A study of the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus). *Biol. Bull. mar. biol. Lab., Woods Hole.* **94**(3): 244–262.

LUNZ, G. R. 1957. Notes on the rock shrimp, *Sicyonia brevirostris* (Stimpson) from exploratory trawling off the South Carolina coast. *Contr. Bears Bluff Labs.* **25:** 1–10.

RENFRO, WILLIAM C. and HARRY L. COOK. 1963. The early larval stages of the seabob, *Xiphopenaeus kroyeri* (Heller). *Fishery Bull. Fish Wildl. Serv. U.S.* **63:** 165–177.

SPRINGER, S. and H. R. BULLIS, JR. 1956. Collections by the OREGON in the Gulf of Mexico. *Spec. Scient. Rept. U.S. Fish Wildl. Serv.* **196:** 1–134.

BEACH CHANGES, ON THE CENTRAL TEXAS COAST ASSOCIATED WITH HURRICANE FERN, SEPTEMBER, 1971

Richard A. Davis, Jr.*

Department of Geology, Western Michigan University Kalamazoo, Michigan 49001

ABSTRACT

Hurricane Fern crossed the central Texas barrier island system on September 10, 1971, imparting a considerable amount of physical energy on gulf beaches. Beach erosion caused pronounced changes in profile configuration. The volume of sediment removed was at least as much as that removed by Hurricane Celia the year before, even though the wind velocity during Celia was three times that of Fern. Partial recovery of the beaches began several days after passage of the storm with shoreward migration and welding of small swash bars.

INTRODUCTION

The role of hurricanes in coastal sedimentation is of great significance, particularly along the northwestern coast of the Gulf of Mexico. During the past decade several studies have been conducted along the Texas barrier island complex in order to gain some insight into the coastal processes and resultant morphology associated with these storms (Hayes, 1965; 1967; Behrens, 1969; Scott, Hoover and McGowen, 1969; McGowen, *et al.*, 1970). Emphasis has been on the role of hurricanes in developing the barrier island system and also on recognition of hurricane generated features in the rock record.

On September 10, 1971, Hurricane Fern passed across the Texas barrier island system of St. Joseph and Mustang Islands. Fern reached hurricane status (winds > 74 mph) on September 7 in the central Gulf of Mexico and moved slowly toward the Rio Grande delta area at a rate of about 5 mph. The following day Fern turned sharply to the north and began moving toward Galveston, Texas. During this period the storm contained maximum winds of about 90 miles per hour making it a rather weak hurricane.

Before Fern reached the Texas coast, she turned again, this time toward the west. The storm began to deteriorate as it approached the barrier island complex and wind velocity declined to the tropical storm level. As the storm moved landward it began to parallel the barrier island system (Figure 1).

Fern moved very slowly along Matagorda and St. Joseph Islands and the eye

* This study was carried out while the author was on sabbatical leave at The University of Texas, Marine Science Institute at Port Aransas.

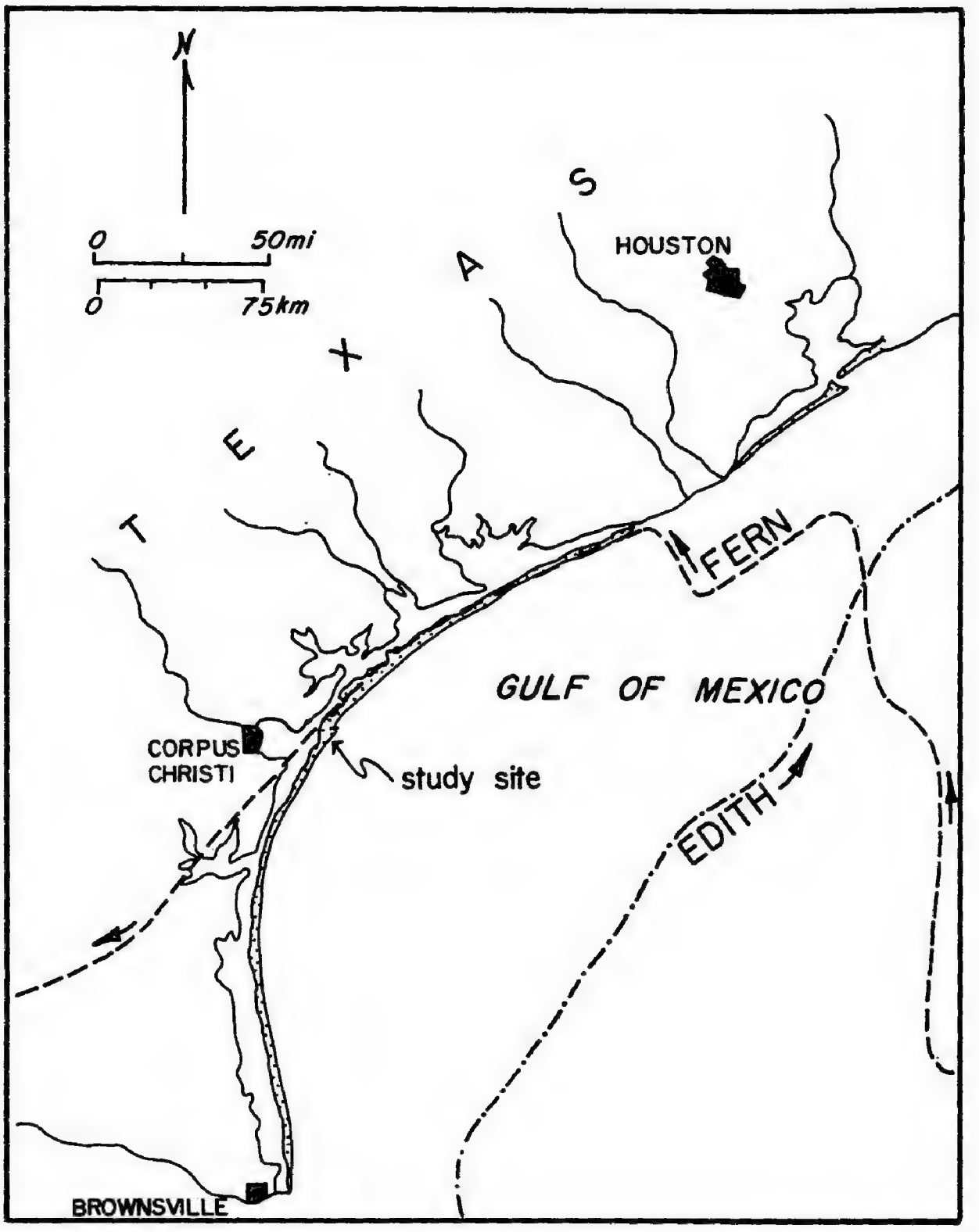

FIG. 1. Map of central Texas coast showing location of study area on Mustang Island and the paths of Hurricanes Edith and Fern.

of the storm passed over the study area near Port Aransas (Figure 1) during the late evening of September 10. Although winds associated with Fern were not high compared to most hurricanes, the slow movement caused significant storm surges and extensive property damage from the heavy rainfall associated with the storm. Storm tides in coastal bays were from 3 to 5 feet (0.9 to 1.5 m) above normal. Most communities along the coast suffered flooding with one town receiving more than 20 inches (>50 cm) of rain in 24 hours.

The only significant geological changes brought about by Hurricane Fern were to the beach and adjacent inner nearshore environment. This study represents a detailed account of storm generated changes and subsequent post-storm recovery

coupled with continuous or closely spaced records of weather, wave and longshore current variation.

PREVIOUS WORK

Hurricanes strike the Texas coast with moderate frequency; 0.67 hurricanes per year since 1900 according to a recent survey (Hayes, 1967). If we extrapolate this rate back in time it is evident that such phenomena must have been significant in the development of the present morphology of the Texas Gulf Coast.

The first detailed observations on the effects of hurricanes along this coast were associated with Hurricane Carla, in September of 1961 (Hayes, 1965; 1967). Carla was one of the most severe storms on record and it caused extreme changes along the barrier island complex. Foredunes were eroded back as much as 300 feet (91.2 m), washover features were prevalent on back-island areas, and storm passes breached the islands at several locations (Hayes, 1967). Much effort was devoted to determining changes in sediment distribution associated with the storm. Effects of a much less intense hurricane, Cindy, which occurred in September, 1963, were also included in Hayes' studies (Hayes, 1967).

Researchers associated with The University of Texas have devoted considerable effort to the study of hurricane generated or associated features. Andrews (1970) investigated a hurricane washover fan in considerable detail. A tidal delta and a river delta, both considerably affected by recent hurricanes were studied by Hoover (1968) and McGowen (1971) respectively. The above studies involved features that were formed or modified by hurricanes Carla and Cindy. More recently Hurricane Beulah, in 1967, struck the Texas barrier islands. Scott, *et al.* (1969) and Behrens (1969) described its effects on the coastal environments from the standpoint of geologic changes and hydrologic changes.

In August of 1970, Hurricane Celia moved onshore at Port Aransas, Texas imparting winds of up to 180 miles per hour. Because of the rapid rate at which the storm moved it did not cause significant geologic changes to the coastal environments although property damage and loss was tremendous (McGowen, *et al*, 1970). Beach erosion at a single location on Mustang Island was determined by pre-storm and post-storm profiles. Up to 1.60 feet (0.49 m) of beach sand was removed during the passage of Hurricane Celia.

CONDITIONS DURING PASSAGE OF FERN

The first influences of Hurricane Fern were felt on Mustang Island during the morning of September 8, 1971. The wind changed direction, from the southeast to the northwest, the velocity began to increase and atmospheric pressure began to decline (Figure 2). During the same time the surf increased and longshore currents were toward the southwest at near 2 feet per second (0.6 m/sec). The occurrence of northwesterly cyclonic winds in the study area on September 8 while the eye of the storm was offshore from Galveston indicates that the radius of Fern in the southwest quadrant was about 200 miles (328 km) at this time.

As the storm moved along the barrier island system toward the study area the barometric pressure continued to drop (Figure 2), wind velocity increased and longshore current velocity declined as winds moved in a generally offshore direction. Maximum sustained wind velocity in the study area was 60–65 miles per hour on both the leading and trailing sides of the low pressure system. These were reached at 2 PM and 11 PM respectively on September 10. The eye of the storm passed through the Port Aransas area between 7 and 9 PM with winds declining to 7 miles per hour. The wind shifted with the passage of the eye and came from the southeast with gradual shifting to the east and northeast (Figure 2).

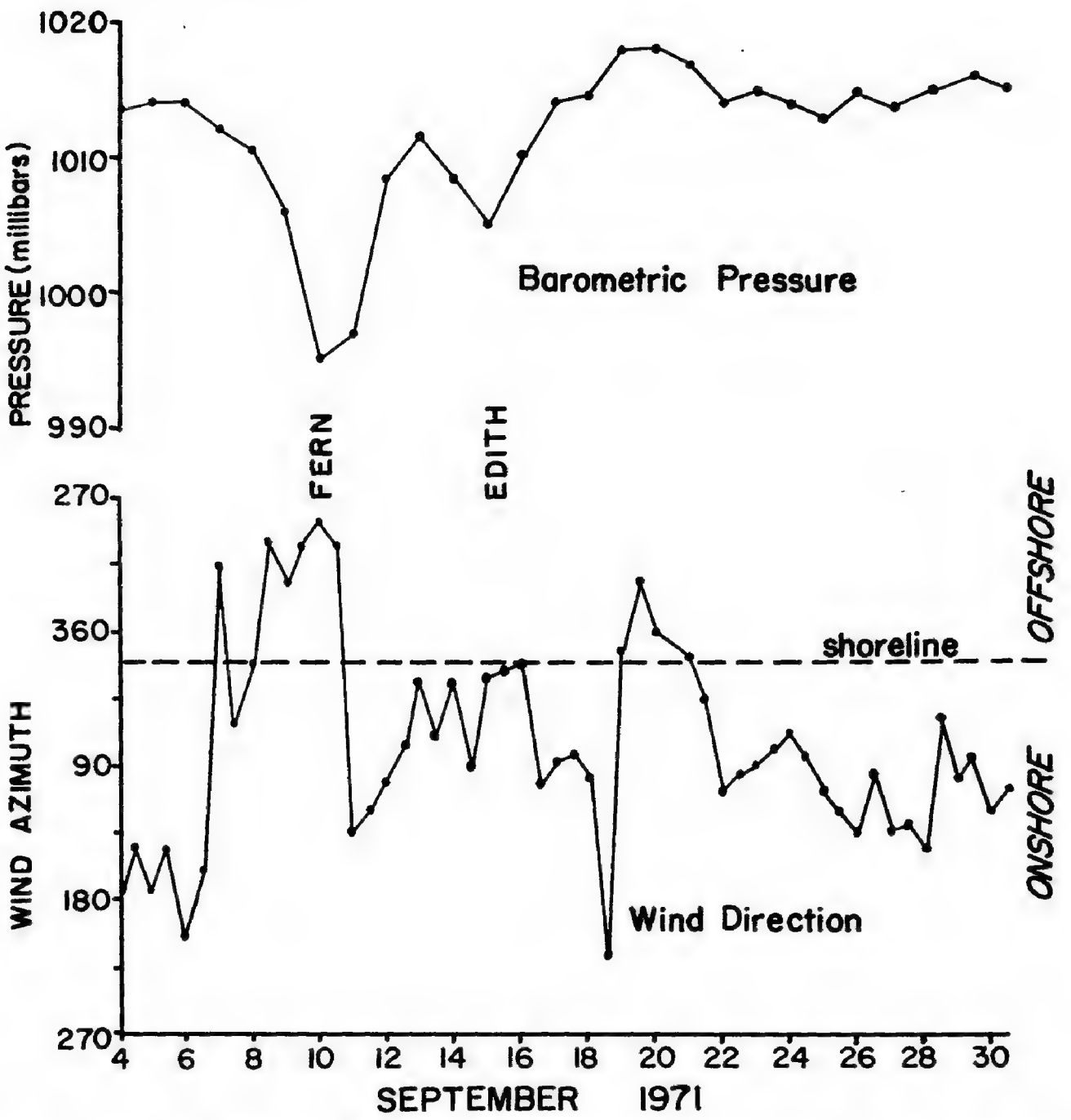

FIG. 2. Temporal variation in barometric pressure and wind direction associated with the passage of Hurricane Fern. Values for barometric pressure are daily means and wind direction is shown at 12 hr. intervals.

Barometric pressure reached a minimum value of 986 millibars during passage of the eye. The steep rise in barometric pressure was accompanied by a change in longshore current direction with slight drift to the north. This is a lag response to the wind shift on the trailing side of the low pressure system. The same relationship has been observed in the Great Lakes (Fox and Davis, 1971).

Hurricane Edith passed to the south of the study area on September 15 (Figure 1). Although the barometer dropped (Figure 2) there were no other noticeable effects of Edith on the central Texas coast.

CHANGES IN BEACH MORPHOLOGY

Beach profiles respond to the overall physical energy imparted by waves and currents. There are essentially two general shapes assumed by the beach; a low energy, accretional profile and a high energy erosional profile (Shepard, 1963). The accretional profile is characterized by a flat, gently landward sloping back-

beach zone, a prominent berm, and a fairly steep foreshore zone. The erosional profile displays a nearly uniform and gently sloping, slightly concave upward profile. There is a pattern to the beach configuration: storms cause rapid erosion, and subsequent quiescent conditions permit the shoreward migration of sand bars which eventually are welded to the beach creating an accretional profile. Observations at two Mustang Island beach locations illustrate both of these profile types associated with Hurricane Fern.

The beaches are located adjacent to Access Road #1, 3 miles (4.8 km) south of Port Aransas, Texas (Figure 1). The two locations are 1500 feet (463 m) apart. Profiles were surveyed from a fence located about 30 to 40 feet (9.3 to 12.4 m) in front of the foredunes. This fence is designed to enhance sand accumulation to rebuild dunes eroded by Hurricane Carla.

PRE-STORM PROFILE

Prior to Hurricane Fern the beach profiles exhibited a typical accretionary shape with a broad backbeach zone and fairly prominent berm located more than 150 feet (46 m) from the baseline. The foreshore zone was about equally wide with a nearly uniform slope which terminated rather abruptly at the plunge step (Figure 3). A small ridge of eolian deposits was present in front of the wind break indicating initiation of dunal development.

POST-STORM PROFILE

Only 24 hours after surveying the pre-storm profiles, there was considerable erosion as waves and longshore currents increased on September 9. Within that period of time the berm had been eroded back more than 50 feet (15 m) at location M-B and over 100 feet (30 m) at location M-A. More than 1.5 feet (0.5 m) of sediment was removed from the beach. Most of this sediment was carried seaward, however a small amount of sediment was transported to the backbeach area by the upsurge of the swash. Profiles surveyed on September 12 portray the post-storm configuration (Figure 3) although erosion conditions still prevailed for the next few days as waves subsided. Both profile locations exhibited essentially the same changes with respect to shape and volume of sediment lost. More than 2 feet (0.6 m) of sediment was removed from the berm area. This exceeds the values recorded for Hurricane Celia in the same area (McGowen, *et al.*, 1970). Although Fern was a rather weak storm, the fact that she moved so slowly allowed for significant storm surge comparable to that of Celia even though wind velocities of Celia were three times greater at the study site.

The area of change is shown by the pre- and post-storm profiles (Figure 3) indicating that at location M-A there was 350 ft.^{2} (32.5 m^2) of sediment removed and 30 ft^2 (2.8 m^2) deposited in the backbeach for a net loss of 320 ft^2 (29.7 m^2). At location M-B there was 370 ft^2 (34.4 m^2) removed and 5 ft^2 (0.46 m^2) of deposition in the backbeach for a net loss of 365 ft^2 (33.9 m^2) (Figure 3). Assuming these values to be representative of the area, this would mean that more than 500,000 ft^3 (>14,000 m^3) of sediment was removed from this 1500 ft (463 m) stretch of beach.

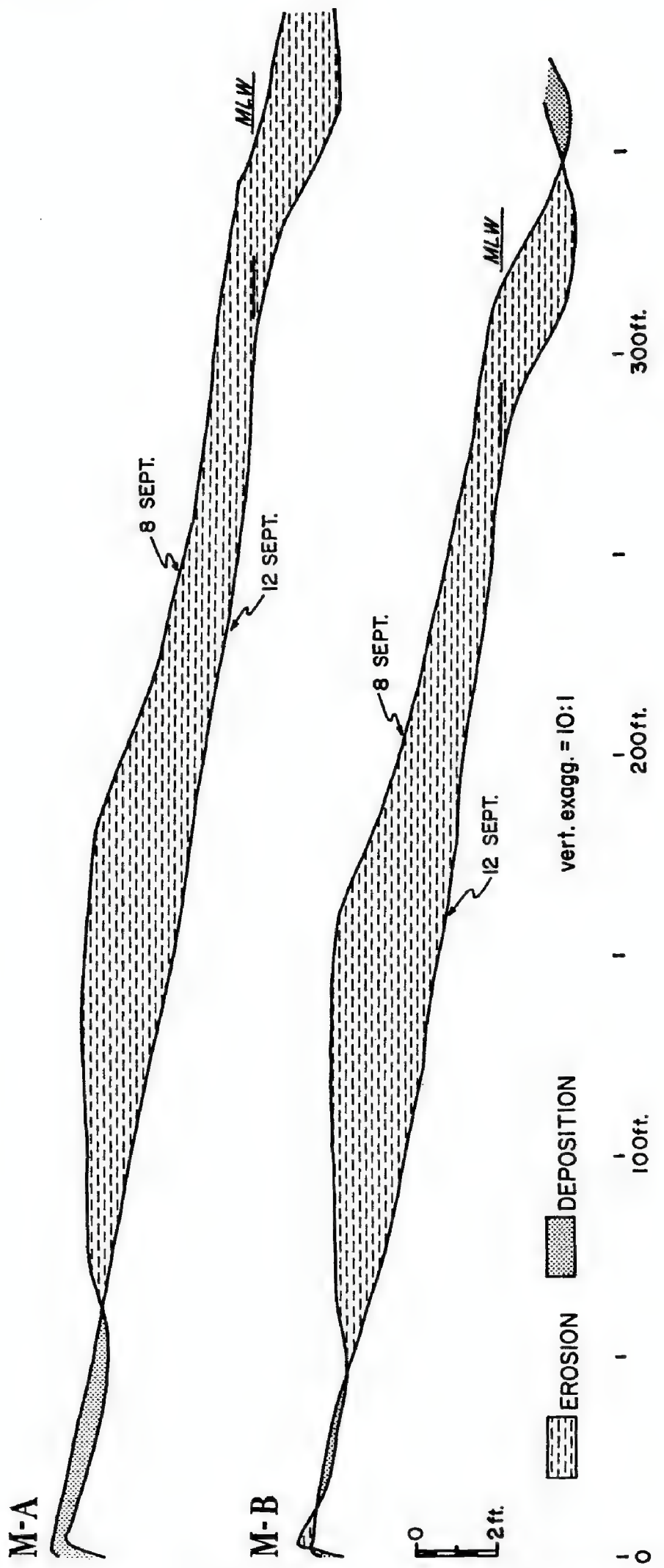

FIG. 3. Pre- and post-storm profiles for beach locations on Mustang Island showing the erosion and deposition associated with Hurricane Fern.

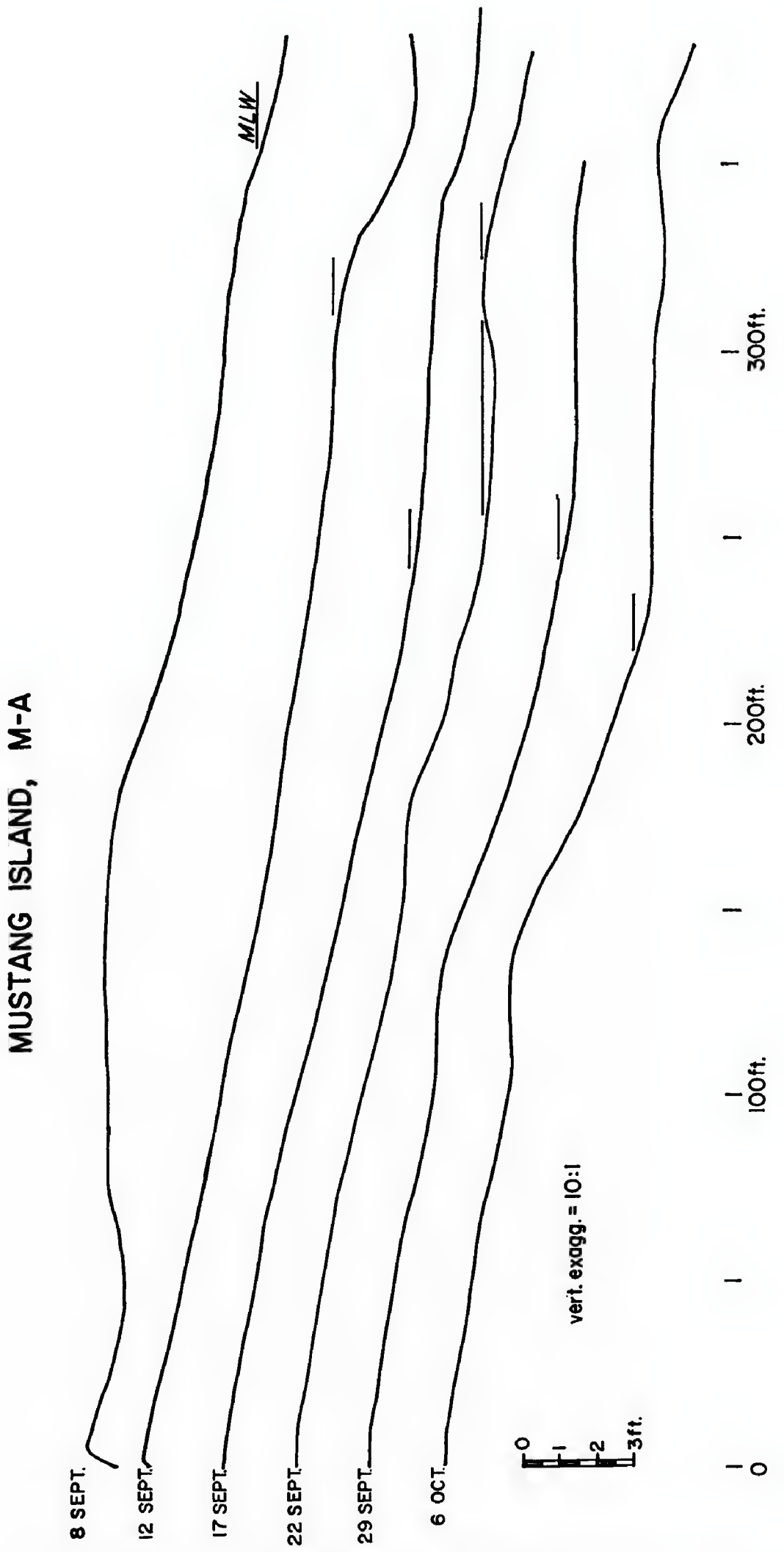

FIG. 4. Beach profiles at location M-A showing pre- and post-storm configuration and recovery profiles after Hurricane Fern.

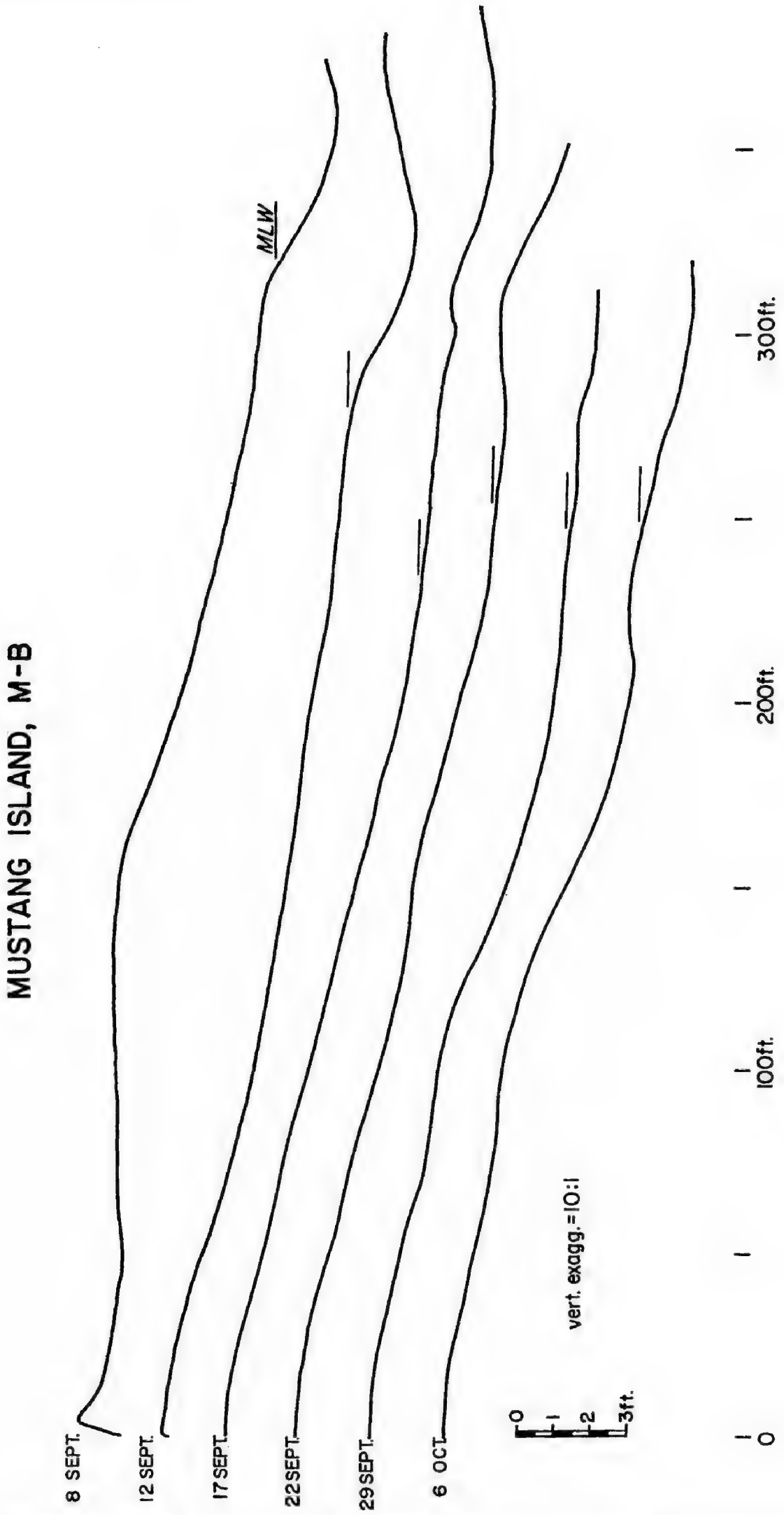

FIG. 5. Beach profiles at location M-B showing pre- and post-storm configuration and recovery profiles after Hurricane Fern.

POST-STORM RECOVERY

The recovery of the beach was slow in starting due to the rather high energy conditions that continued for several days after the passage of Fern. Post-storm recovery was enhanced by the occurrence of a "norther" on September 16–18. The offshore winds generated by these weather systems tend to dampen wave activity. As a result the small waves move sediment landward. A migrating sand bar or swash bar was present on September 22 (Figures 4 and 5). During the succeeding two weeks there was further migration of this sand bar with eventual welding to the beach and subsequent formation of other migrating bars (Figures 4 and 5).

The recovery processes may return the beach to its pre-storm profile, however it will require considerable time. If similar storms occur with increasing frequency the beach will not be allowed to recover. It may take a year for nature to repair the destruction caused by a single storm and in case of very damaging storms like Hurricane Carla, there may never be complete recovery.

SUMMARY

Based on the data associated with Hurricane Fern and that presented by previous investigators, the following general statements are appropriate for hurricane generated beach changes:

1) The total volume of sediment loss resulting from such a storm is large and accounts for most of the longterm erosion along the relatively low energy barrier island beaches of central Texas.

2) The rate of movement of the storm is one of the most significant factors in beach erosion. Slow moving storms generate large waves and high storm tides which are the most important factors in beach erosion.

3) Post-storm recovery of the beach is quite slow and may not be completed before the next severe storm arrives.

ACKNOWLEDGMENTS

The University of Texas, Marine Science Institute is acknowledged for providing facilities during the study period. E. William Behrens of the Institute staff supplied the weather records. M. A. Davis assisted during most of the data collection.

LITERATURE CITED

ANDREWS, P. B. 1970. Facies and genesis of a hurricane-washover fan, St. Joseph Island, central Texas coast. *Univ. of Texas Bur. Econ. Geology Rept. Inv.* No. **67:** 147 p.

BEHRENS, E. W. 1969. Hurricane effects on a hypersaline bay. Lagunas Costeras, un Simposio. *Mem. Simp. Intern. Lagunas Costeras.* UNAM-UNESCO, Mexico, D.F.: 301–312.

FOX, W. T. and R. A. DAVIS. 1971. Fourier analysis of weather and wave data from Holland, Michigan, July 1970. *Tech. Rept.* No. **3**, ONR Contract 388–092, 79 p.

HAYES, M. O. 1965. Sedimentation in a semiarid, wave dominated coast (south Texas); with emphasis on hurricane effects. Ph.D. thesis, Univ. of Texas, Austin, 350 p.

————. 1967. Hurricanes as geological agents: case studies of Hurricanes Carla, 1961, and Cindy, 1963. *Univ. of Texas Bur. Econ. Geology Rept. Inv.* No. **61:** 54 p.

HOOVER, R. A. 1968. Physiography and surface sediment facies of a Recent tidal delta, Harbor Island, central Texas coast: Ph.D. Thesis, Univ. of Texas, Austin, 184 p.

McGOWEN, J. H. (1971). Gum Hollow fan delta, Nueces Bay, Texas. *Univ. of Texas Bur. Econ. Geology Rept. Inv.* No. **69**: 91 p.

————, C. G. GROAT, L. F. BROWN, JR., W. L. FISHER and A. J. SCOTT. 1970. Effects of Hurricane Celia—a focus on environmental geologic problems of the Texas coastal zone. *Univ. of Texas Bur. Econ. Geology Geol. Circ.* **70–3**: 35 p.

SCOTT, A. J., R. A. HOOVER and J. H. McGOWEN. 1969. Effects of Hurricane Beulah, 1967, on Texas coastal lagoons and barriers. Lagunas Costeras un Simposio. *Mem. Simp. Intern. Lagunas Costeras*. UNAM-UNESCO, Mexico, D.F.: 221–236.

SHEPARD, F. P. 1963. Submarine geology. Harper and Row, N. Y., 557 p.

SILICA CONTENTS IN THE NORTHWESTERN FLORIDA GULF COAST

Carol F. Stephens and Carl H. Oppenheimer

Department of Oceanography, Florida State University

ABSTRACT

Analyses of the river and bay waters of the Northwestern Florida Gulf Coast indicate that weathering of silica is active and that the fresh waters and runoff are significant sources of silica for the estuarine waters. An eighteen month study of the distribution of silica in the St. Marks River and Apalachee Bay indicates that active inorganic processes contribute to the loss of silica as dilution is not entirely responsible for the change. Silicate content of the surface waters ranged from 240 ug-at/1 in fresh water at 10 miles from the open Apalachee Bay to less than 1 ug-at/1 in the Bay where salinity is 34 ‰. The St. Marks River has an average discharge of 1000 cfs which, if containing 200 ug-at Si/1, would have an average discharge of approximately 15.5 metric tons of silica per day. Other areas of the shore estuarine environment show similarly high silica values and are relative to salinity.

INTRODUCTION

Chemical weathering in terrestrial environments produces dissolved ions such as silicate that contribute to seawater salinities. Because of the high content of silicate, up to 240 ug-at/l, in the St. Marks River, Wakulla County, Florida, and the significance of silica, as a nutrient for phytoplankton growth, for clay mineral formation, and as a buffering agent, a study was initiated in the St. Marks River estuary to determine the dissolved silica distribution in the transition between fresh water and seawater. The St. Marks is a short river made up of artesian and swamp water which flows into an open bay or estuary (Figure 1). Our studies and studies of the Mississippi River estuary (Bien, Contois, and Thomas, 1958) indicate that inorganic removal of silica occurs during mixing of river and seawater, while studies of the Columbia River estuary (Richards, 1958) show no evidence of silica removal during mixing. Because of the possible importance of mineral water reactions as a control on the silica content of ocean water (Garrels and Mackenzie, 1967), the rate of silica removal in estuaries must be established, and especially those areas where silica is added in high quantities.

The high silica content of the waters of Florida near St. Marks may be attributed to many factors but no known general solution reaction has been proposed. The loss of soluble silica due to processes other than dilution during the transition between fresh and seawater remains a matter of speculation. The change in pH during the water transition, although not large, may have a pronounced effect

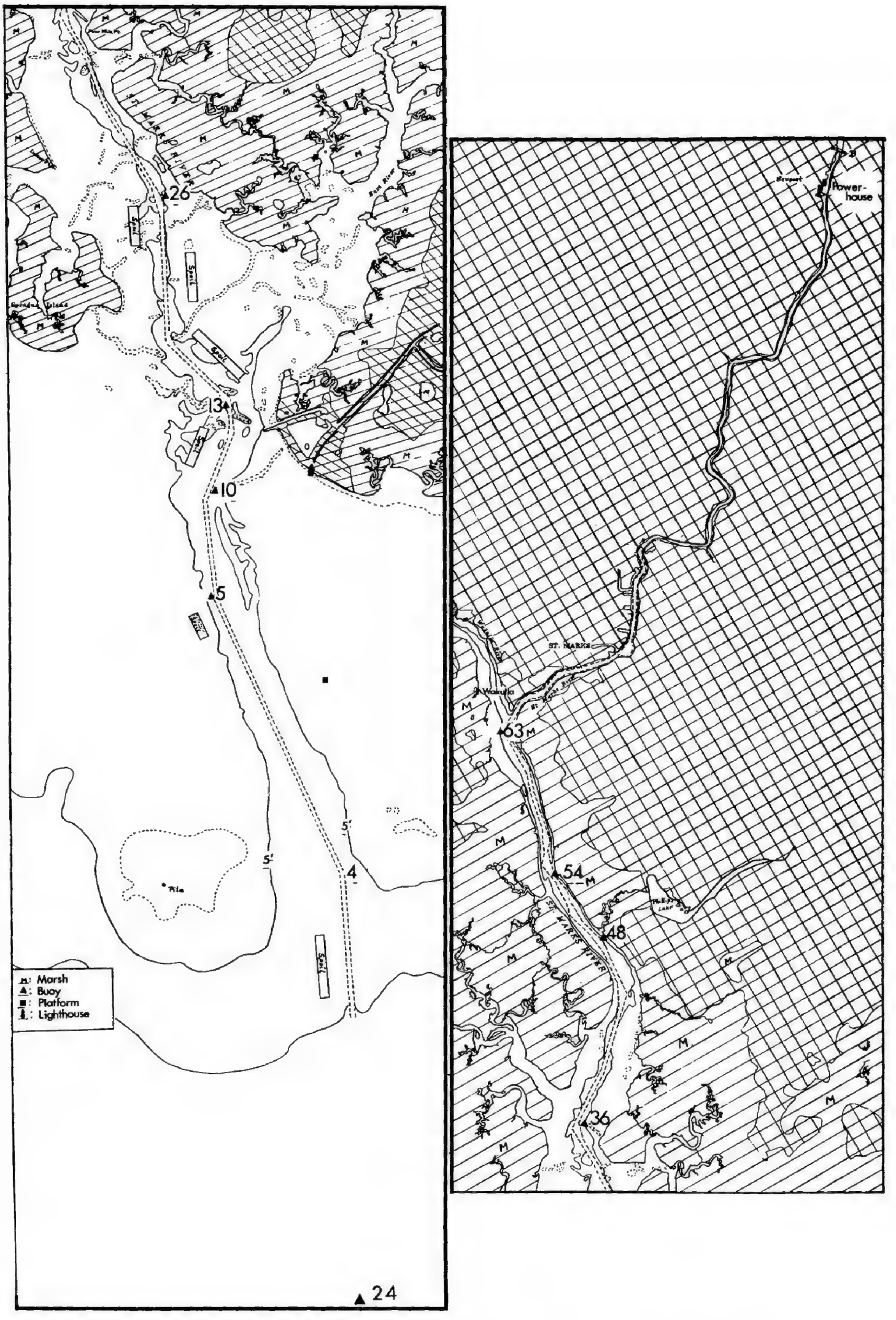

FIG. 1. Chart of St. Marks River, Florida, with Station Locations.

on many chemical processes such as the colloidal states or precipitation. Clay minerals may be formed or the silica may change from the dissolved to colloidal state as proposed in discussions of silica reactions (Okamoto, Okura and Goto, 1957). Silica may also be removed from the water through biological fixation by diatoms and other organisms.

Garrels (1965), described a reversible reaction in which dissolved silica and degraded silicate minerals can participate in the fixing of silica and alkali metal cations, with the release of hydrogen ions, resulting in the regulation of pH of natural waters. In this reaction feldspar reacts with carbon dioxide in water to yield sodium ions, bicarbonate ions, kaolinite, and silicate.

$$2\,NaAlSi_3O_8 + 2\,CO_2 + 3\,HOH =$$
$$2\,Na^+ + 2\,HCO^-_3 + Al_2Si_2O_5(OH) + 4\,SiO_2$$

Silica is found suspended in natural water in three forms: ionic, colloidal, and as biological precipitates. There is considerable evidence that silica exists in solution in water in monomeric form, possibly hydrated monosilicic acid, $Si(OH)_4$. Weitz, Franch, and Schuchare (in Iler, 1955) have found that silica in the monomeric state, as indicated by the freezing-point method, will react with molybdic acid completely within 75 seconds at 20°C., while disilicic acid reacts completely in about 10 minutes, and higher polysilicic acids require still longer time (Iler, 1955).

This investigation concerns the "reactive silicate" as determined by the yellow silicomolybdate complex reaction of silicate with molybdic acid which is reduced to a blue colored complex, as described by Strickland and Parsons in their *Manual of Sea Water Analysis* (1965). This method requires that the test solution remain in contact with molybdic acid for from 10 minutes to no more than a half hour. Since most of the color development takes place in the first two minutes of the reaction, the material called "soluble silicate", measured in this experiment, is probably mostly mono- and disilicic acid. Although this procedure may not show all silicic acid present, it probably gives a meaningful measurement of that available to growing plant cells and fast chemical reactions.

DESCRIPTION OF THE AREA

The St. Marks River, about 19 miles south of Tallahassee, Florida enters with an average discharge of 1000 cfs. a broad estuarine area in Apalachee Bay (Figure 1). The water basin area of the St. Marks, about 11 miles upstream from the confluence with the Wakulla River, is 540 square miles and includes 290 square miles of area draining into Lake Miccosukee which contributes to the St. Marks River at high water stages. The river channel is lined in many places with Miocene limestone. The sample stations are labeled in Figure 1 as follows:

> Bridge (B), Powerhouse (P), Wakulla River (W) and buoy numbers down the river to Buoy 24 of the Intracoastal water way approximately 15 miles from the river mouth.

At the bridge, tidal infiltration of seawater is very slight and the water is fresh. Buoy 24, the outer area of the bay, has an oceanic salinity of 34‰. The tidal amplitude is 2–3 feet.

The estuarine and bay areas are shallow with a complex system of reefs and shoals as shown by the contours in Figure 1. The river channel is approximately 15 feet deep at mean low water up to the Newport Bridge (Figure 2). Buoy 24 has a depth of approximately 30 feet. The Wakulla River, originating from Wakulla Springs, an artesian flow, enters at Buoy 63. Springs are the principle source of the Wakulla River, while runoff from swampy areas is the principle source of the St. Marks River, with springs as secondary sources.

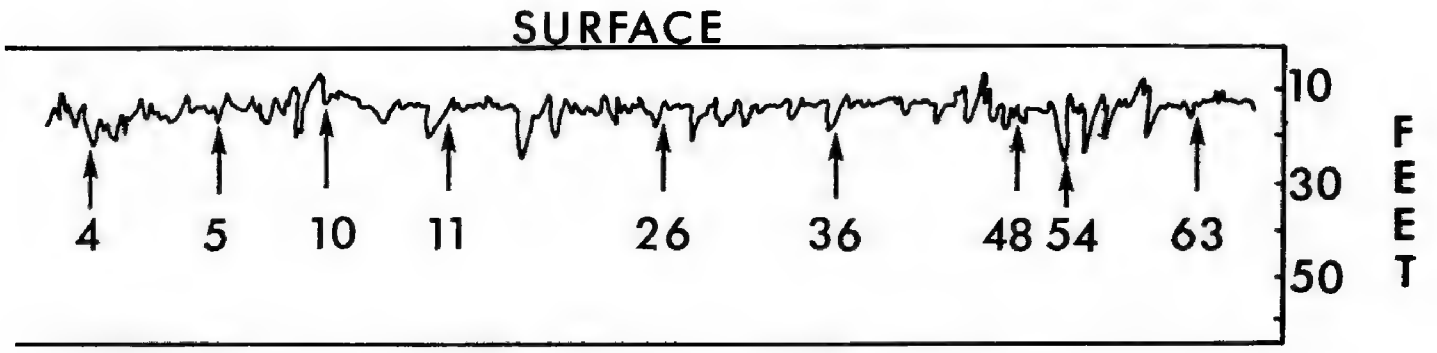

FIG. 2. Fathometer Bottom Contours from Buoy 4 to 63, St. Marks River.

The St. Marks water usually has high humin and tannin content which produces a deep reddish brown color that varies during the year. These materials may act as complexing agents as they pass from the colloidal (fresh water) to particulate phase (seawater) during the transition in salinity and pH. The pH of the waters ranges from 7.45 upstream to 8.8 in the Bay. The temperature range of the St. Marks River water is 10 to 18°C in winter and 23 to 30°C in summer.

MATERIALS AND METHODS

Samples were taken monthly at the series of stations for approximately 18 months. Other areas in the surrounding local were also sampled for comparison.

Each series of water samples was collected in plastic bottles as rapidly as possible to prevent large variations due to tidal changes. The approximate time between sampling from Buoy 4 to the powerhouse was one-half hour. The time required to obtain samples between Buoys 4 and 24 was one additional hour, but the effects of tidal changes in this latter area can be considered negligible.

Surface samples were taken by hand and bottom samples by Niskin Biological Samplers. Salinity and pH were determined respectively with a Hy-Tech induction salinometer and a Sargent pH meter.

The water samples were stored on the boat on ice in darkness to decrease uptake of silica by growing diatoms. Samples were returned to the laboratory within 6 hours from sampling and refrigerated at 2°C. The silica analyses were completed within three days. It was experimentally determined that no significant change in silica content occurred during the time between sampling and analysis.

Silica was determined by the procedure in Strickland and Parsons (1965) and corrected for salinity. Silicate for duplicate samples did not vary more than 1 ug-at/1 for high values and was negligible below 10 ug-at/1.

RESULTS

Silicate content of the surface waters ranged from 240 ug-at/l at the Bridge to less than 1 ug-at/l at Buoy 24 and is subject to seasonal variations as shown in Figures 3 and 4, with the highest concentrations in April and September and the

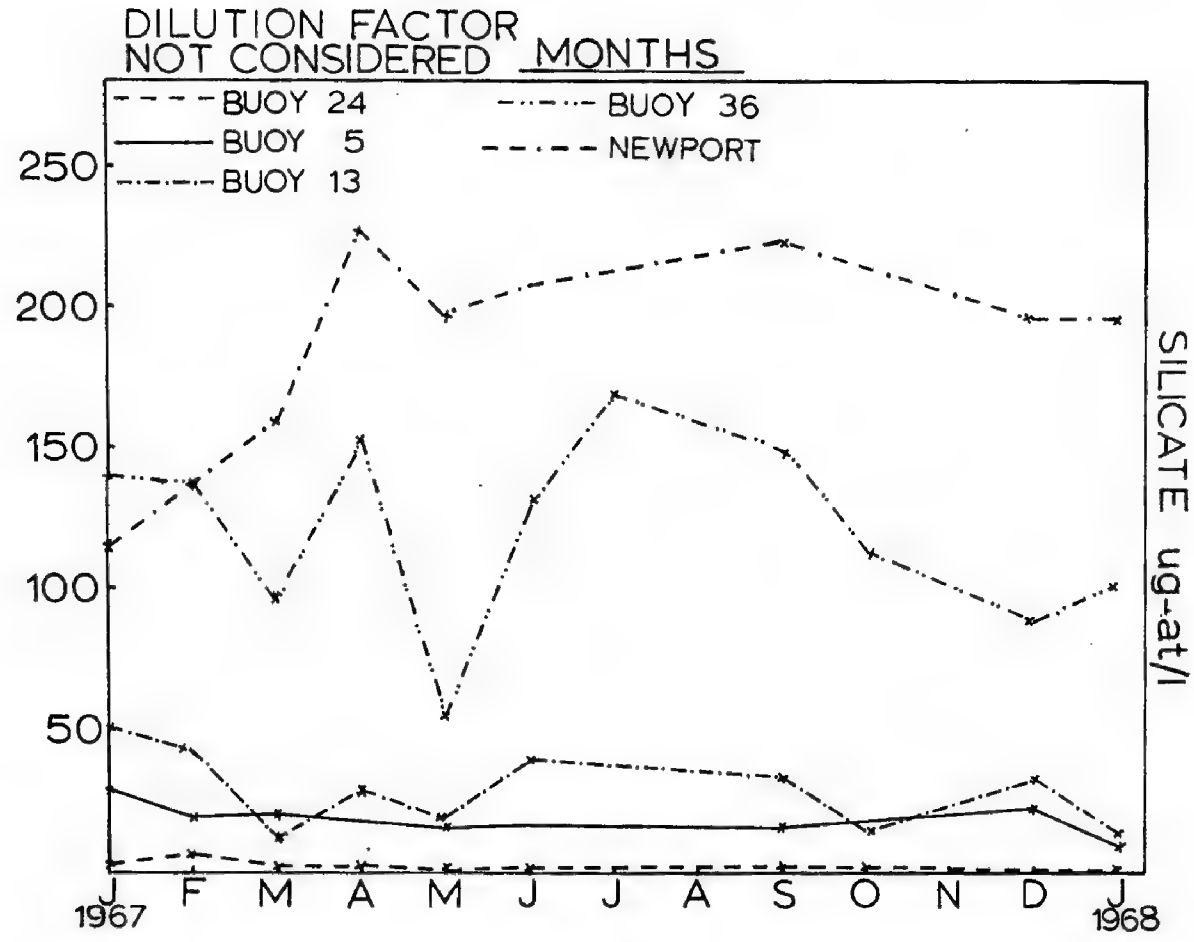

FIG. 3. Seasonal Variations in Silicate *not* Considering the Dilution Factor.

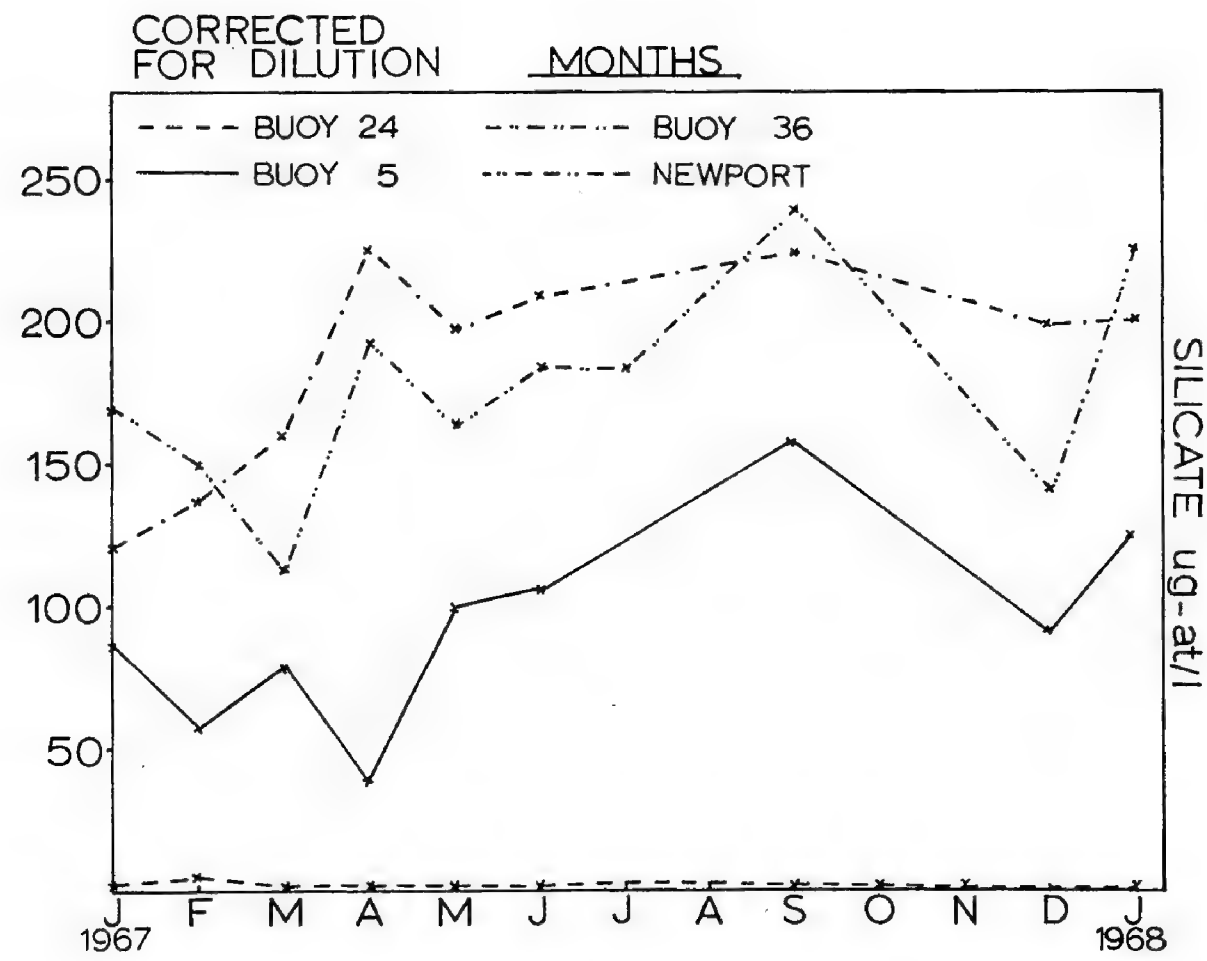

FIG. 4. Seasonal Variations in Silicate Considering Dilution Factor.

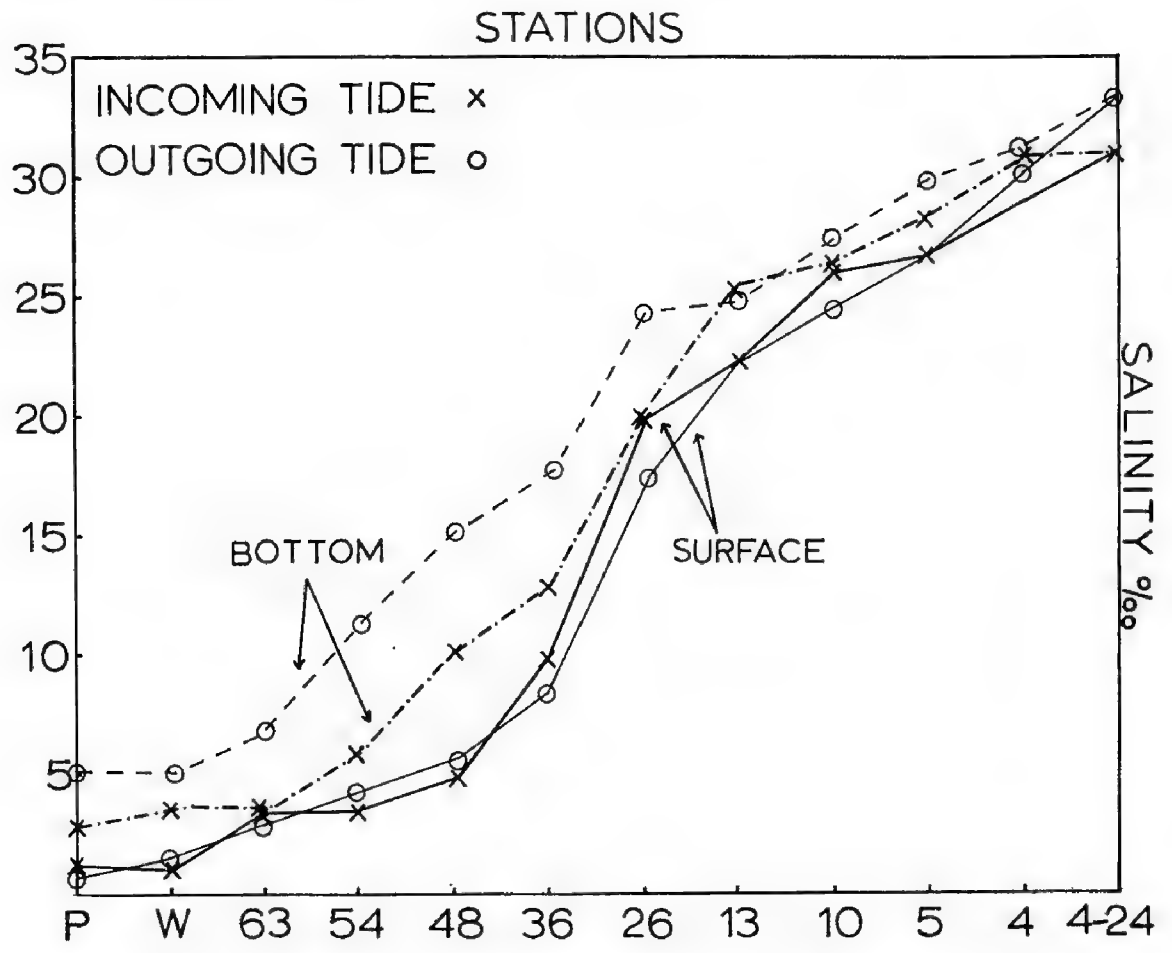

FIG. 5. Salinity, Surface and Bottom, on Incoming and Outgoing Tide.

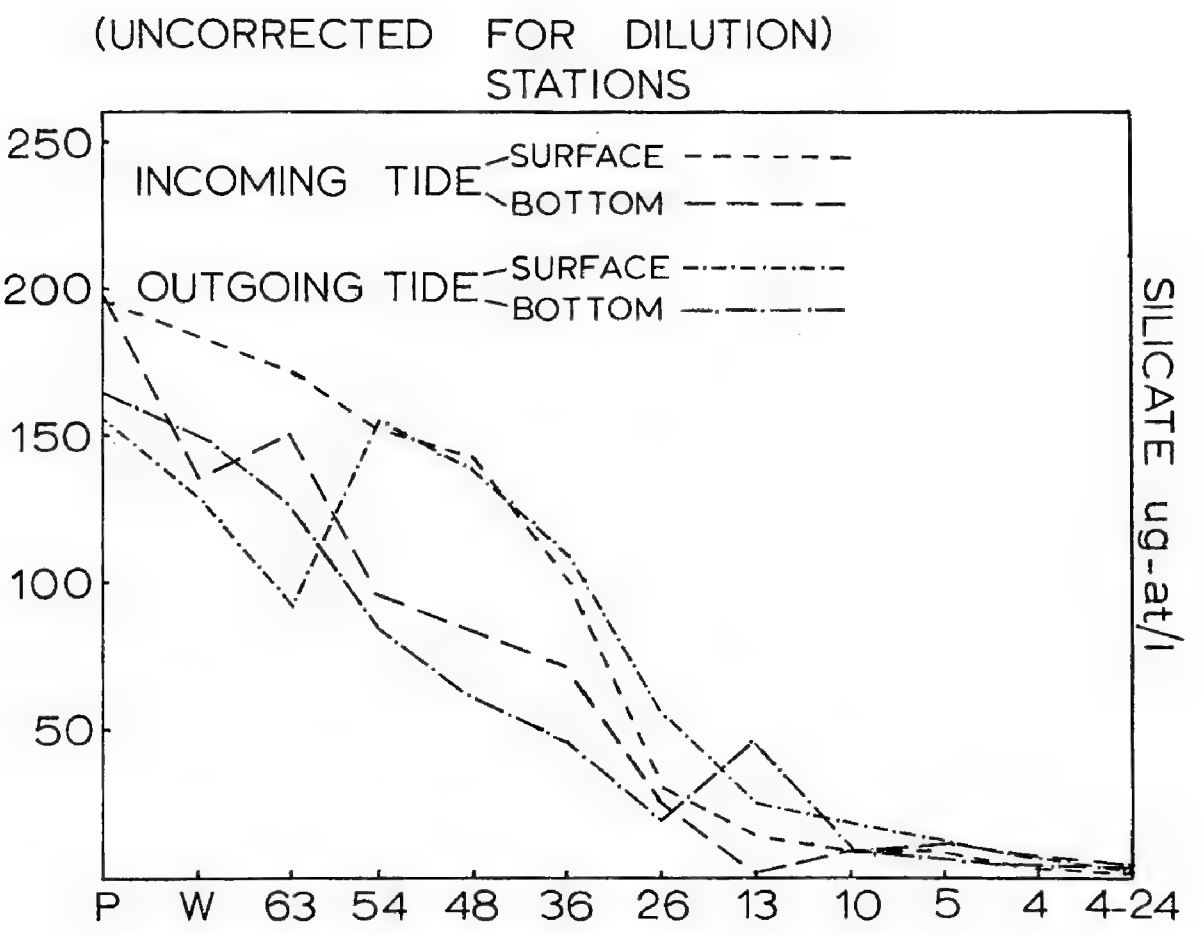

FIG. 6. Silica, Surface and Bottom, on Incoming and Outgoing Tide.

lowest in March and December. Seasonal variation is not pronounced in the open Apalachee Bay waters from Buoy 4 to Buoy 24, as the rather low silicate ion concentration remains rather stable within the range 0.5 to 3 ug-at/l at Buoy 24. Silicate appears to vary inconsistently with depth (Figures 5 and 6), apparently a function of rain, tide and wind mixing and mixing due to the irregular river bottom and channel.

The incoming tide brings saline waters of lower silicate content into the estuary. As shown by the bottom contours of the river in Figure 1, and the bottom and top salinities (Figure 5) there is a strong mixing effect at those points where abrupt pinnacles are followed by relatively deep basins. Such areas, near Buoys 10, 26, and 63 have approximately equal silicate concentrations and salinities in both surface and bottom waters showing a mixing effect. The relationship between salinity and silicate concentrations does not exist during the receding tide, as shown by Figures 5 and 6. Figure 6 shows the extent of dilution as a function of tidal effects and water depth and indicates that the fresh surface water does retain its identity.

The data for November, 1966 and March, 1967 are shown in Figures 7 and 8. Reactive silicate decreases rapidly with increase in salinity. Representative silicate versus salinity data are plotted (Figure 9), and compared with the straight line that would be obtained if dilution were the only mixing effect. The values deviate from this line, indicating that other factors than dilution must be involved. According to Okamoto, Okura, and Goto (1957), the optimum pH for the precipitation of molecularly dispersed silica is about 8. The pH ranges, from 7.45 upstream to 8.80 in the Bay, indicate optimal conditions for precipitation of saturated compounds when the fresh and salt water masses meet.

Bien, Contois, and Thomas (1958), in their study of the Mississippi River concluded that simple dilution does not account for the silica decrease they observed. Values for reactive silicate in the fresh water of the Mississippi River range from 66.6 to 124.9 ug-at/l, indicating that the St. Marks and Wakulla Rivers contain considerably more dissolved silica than the Mississippi River. The St. Marks discharges an average of 1000 cfs which, if containing 200 ug-at Si/l, would have an average discharge of approximately 15.5 metric tons of silica per day.

During the period of this survey, silica determinations were made in a wide variety of environments in the vicinity of the St. Marks River (Table 1) from fresh water to seawater. These data show that adjacent rivers, such as the Wacissa and Fenholloway, have silica values up to 278 ug-at/l and are similar to bays such as Alligator Harbor, where considerable rain water runoff is present and in which silica values up to 273 ug-at/l were observed. The high values in the rivers and bays decreased through dilution with seawater to values of less than 1 ug-at/l in salinities of 32‰ just a mile or two away from the coast and mouth of the rivers or bays. About 50 linear miles of shore line were surveyed (Table 1). It is interesting to note the large variations as affected by time of collection, runoff, shore changes, rivers, etc., shown in Table 1. Large temporal varaitions were found in Alligator Harbor, especially at the head where values were 272 to 70 ug-at Si/l respectively, one week apart.

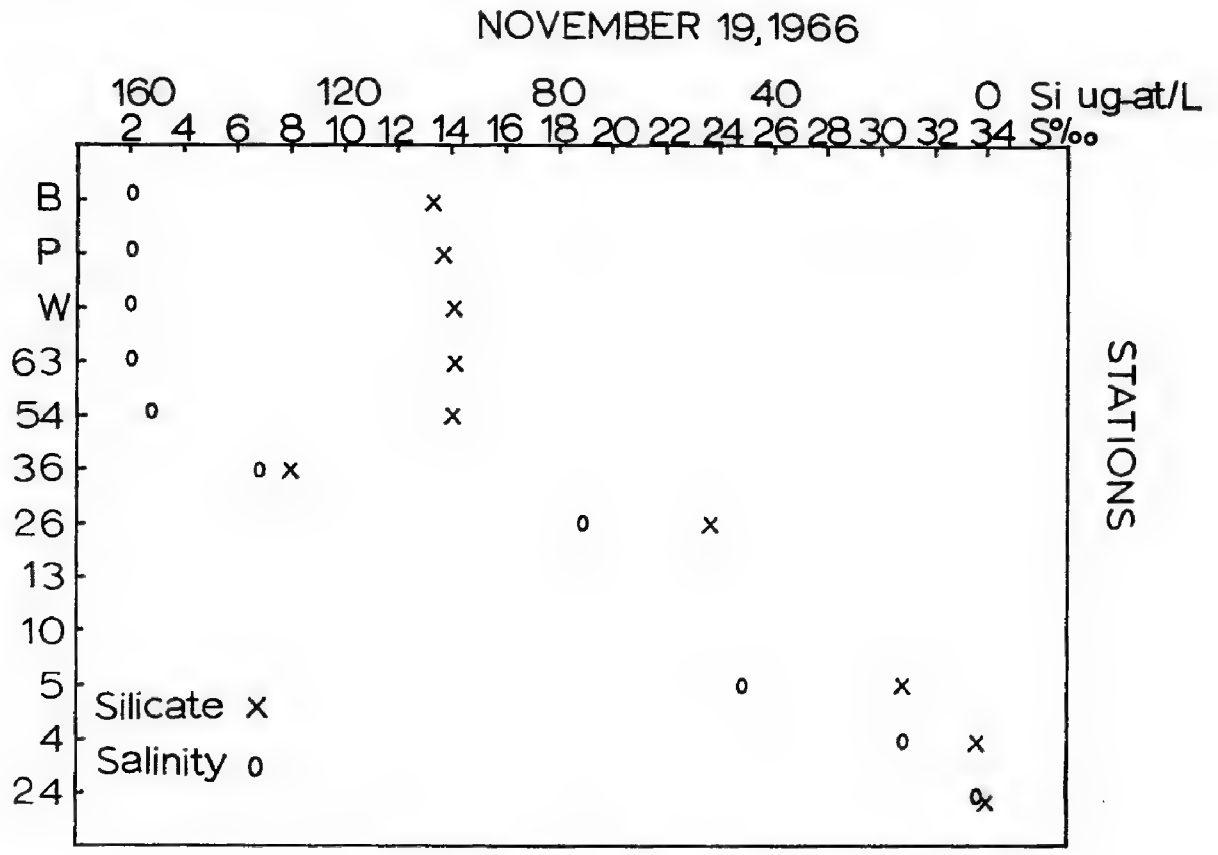

FIG. 7. Silica and Salinity Data for November 19, 1966.

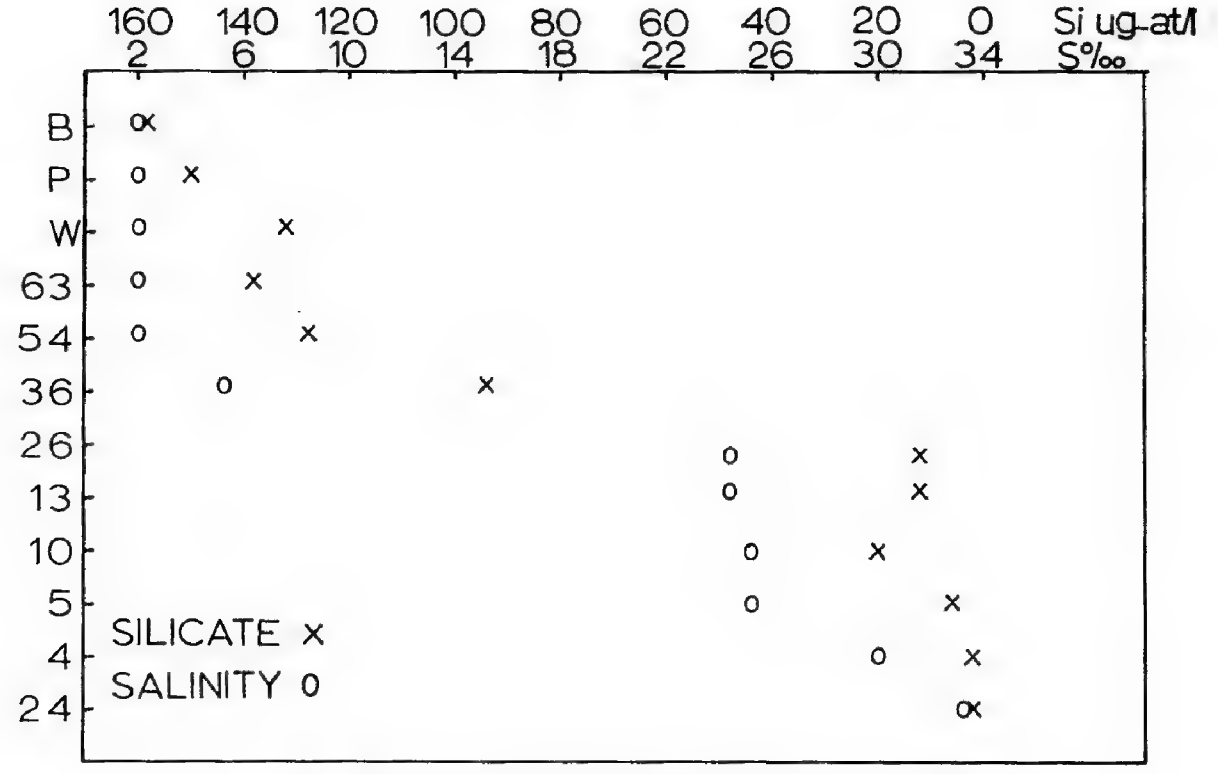

FIG. 8. Silica and Salinity Data for March 3, 1966.

DISCUSSION

The fresh waters of the rivers and bays of the Florida Coast near St. Marks have high silica contents which exceed 250 ug-at/l. When this fresh water is diluted with seawater the silica content decreases at a faster rate than can be accounted for by simple dilution (Figure 9). Inorganic precipitation or colloid formation may be the primary cause of the loss of silica from solution. The fresh waters are lower in pH than the seawater and usually have a high content of

TABLE 1

Surface silicate values

Location	Date	Water depth	Salinity	ug-at Si/L
Wacissa River source (spring)	7–16–66	10 ft.	Fresh*	278
Wacissa River 2½ mi. from spring, downstream	7–16–66	4 ft.	Fresh	188
Wacissa River 2 mi. above Aucilla River	7–16–66	5 ft.	Fresh	140
Aucilla River	7–16–66	. .	Fresh	134
Aucilla-Wacissa River Junction	7–16–66	. .	Fresh	81
Wakulla River	11–19–66	15 ft.	Fresh	116
Suwannee River, 70 mi. from the Gulf of Mexico	4–26–68	30–40 ft.	Fresh	172
Suwannee River, mouth	4–26–68	. .	Fresh	135
Spring at Branford on Suwannee River	4–26–68	. .	Fresh	100
Suwannee River, Buoy 4	. . . . .	5 ft.	24.8‰	20
Fenholloway River	7–15–66	. .	Fresh	112
Lake Bradford	7–10–66	6 ft.	Fresh	1.5
Lake Bradford, Sediment surface 5 cm	7–10–66	1 ft.	. . . .	184
Lake Bradford, Sediment 10 to 15 cm depth	7–10–66	. .	. . . .	54
Alligator Harbor, head, in marsh	8–3–66	3 ft.	31.1	225
Alligator Harbor, head	8–3–66	4 ft.	30.9	79
Alligator Harbor, half-way out	8–3–66	5 ft.	31.0	41
Alligator Harbor, mouth	8–3–66	8 ft.	31.8	31
Off Alligator Point about 3 miles	7–22–66	30 ft.	34.1	1.0
Turkey Creek, stream entrance	7–22–66	2 ft.	32.3	17
Turkey Point, Basin	7–22–66	2 ft.	21.8	14
Off Turkey Point one-fourth mile	7–22–66	6 ft.	29.9	8.5

colloidal and soluble humic acids and iron. As these two latter materials reach the seawater they are rapidly precipitated. It is possible that co-precipitation may account for the decrease in silica over dilution. It is unlikely that the indigenous diatom populations of 100,000 per liter (personal communication, Glooschenko) could appreciably affect the large concentrations available from the river water to account for losses over dilution.

Three mechanisms are likely to be involved in the silica loss: (1) reaction of silicate with electrolytes, especially cations, resulting in mineral formation; (2) adsorption or co-precipitation with suspended solids or colloidal materials in water and sediment; and (3) co-precipitation with humic acids as they enter the seawater and are changed from colloidal to particulate form. The low values of Apalachee Bay of 0.5 to 2.5 ug-at/l are comparable to Richards data (1958) for the Caribbean and appear to be somewhat low for estuarine environments. Unpublished data from an FSU-Eastward cruise in 1969 showed that the open Gulf of Mexico had silicate values of less than 1 ug-at/l.

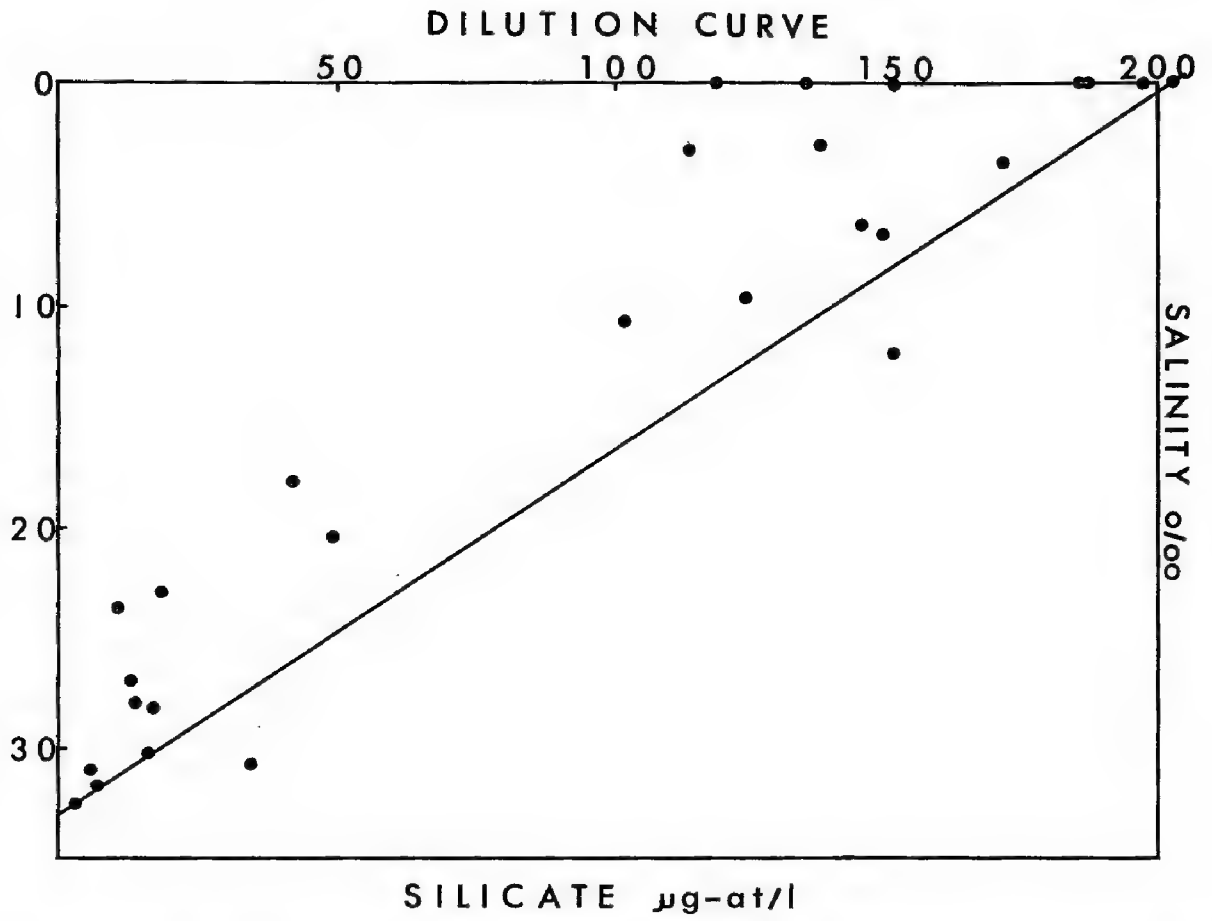

FIG. 9. Calculated Dilution Curve for Silicate Shown by Straight Line and Silicate Values Obtained.

LITERATURE CITED

BIEN, G. S., D. E. CONTOIS and W. H. THOMAS. 1958. The removal of soluble silica from fresh water entering the sea. *Geochim. cosmochim. Acta.* **14:** 33–55.

GARRELS, R. M. 1965. Silica: Role in the buffering of natural waters. *Science, N. Y.* **148** (3666): 69.

GARRELS, R. M. and F. T. MACKENZIE. 1967. Origin of the chemical compositions of some springs and lakes. In Werner Stumm (ed.) *Equilibrium Concepts in Natural Water Systems*, Amer Chem. Soc.

ILER, R. K. 1955. *The Colloid Chemistry of Silica and Silicates.* Cornell University Press, Ithaca, New York. 324p.

OKAMOTO, G., T. OKURA and K. GOTO. 1957. Properties of silica in water. *Geochim. cosmochim. Acta.* **12:** 123–132.

RICHARDS, F. A. 1958. Dissolved silicate and related properties of some Western North Atlantic and Caribbean waters. *J. mar. Res.* **17:** 449–465.

STRICKLAND, J. D. H. and T. R. PARSONS. 1965. A Manual of Sea Water Analysis. *Bull. Fish. Res. Bd. of Can.* **125:** 67–72.

THE DISTRIBUTION OF DISSOLVED ORGANIC MATTER IN THE NEAR-SHORE WATERS OF THE TEXAS COAST

Larry G. Maurer* and P. L. Parker

University of Texas, Marine Science Institute, Port Aransas, Texas 78373

ABSTRACT

The concentration of dissolved organic matter in the coastal waters of South Texas, estuaries and shelf, was measured. Zones of high and low concentration were found on the shelf. The concentrations in the estuaries (2–5.3 mg/lt) were higher than those for shelf waters (1–3.7). A new analytical method based on persulfate oxidation and gas chromatographic detection was developed.

INTRODUCTION

A small fraction of the organic matter produced in marine waters escapes immediate oxidation so that a substantial concentration accumulates in the water column. In general dissolved organic matter, that organic matter which passes a 0.45 μ millipore filter, accounts for the major part of this material. This is especially the case for the open sea, but even in inshore waters approximately one-half of the organic matter in the water is dissolved.

The chemical nature, rates of recycling and concentrations of organic material is of interest to chemists and biologists because of the influence it has on living and non-living processes in the sea. Menzel and Ryther (1970) have reviewed the subject of organic matter in the oceans. A great deal of effort has gone into establishing the world wide concentrations of dissolved and particulate organic matter (POM) in the open sea. Fredericks and Sackett (1970) summarized our knowledge of the distribution of organic matter in the Gulf of Mexico. They report that the concentration of dissolved organic matter of shelf waters ranges between 0.58 and 2.35 mg C/liter (79 samples). The purpose of our study was to establish the fine structure of these concentration ranges for the shelf off the Texas Coast. We had not expected to find the concentration zones which are herein reported.

MATERIALS AND METHODS

(SAMPLES)

The sampling stations in the Texas estuaries and coastal waters are shown in Figures 1 and 2. Their locations are listed in Tables 1–3. Gulf of Mexico samples were taken from 2–5 meters below the surface with one or two liter Van Dorn samplers, and then immediately suction filtered

* Present address: Department of Oceanography, Texas A&M University, College Station, Texas.

FIGURE 1

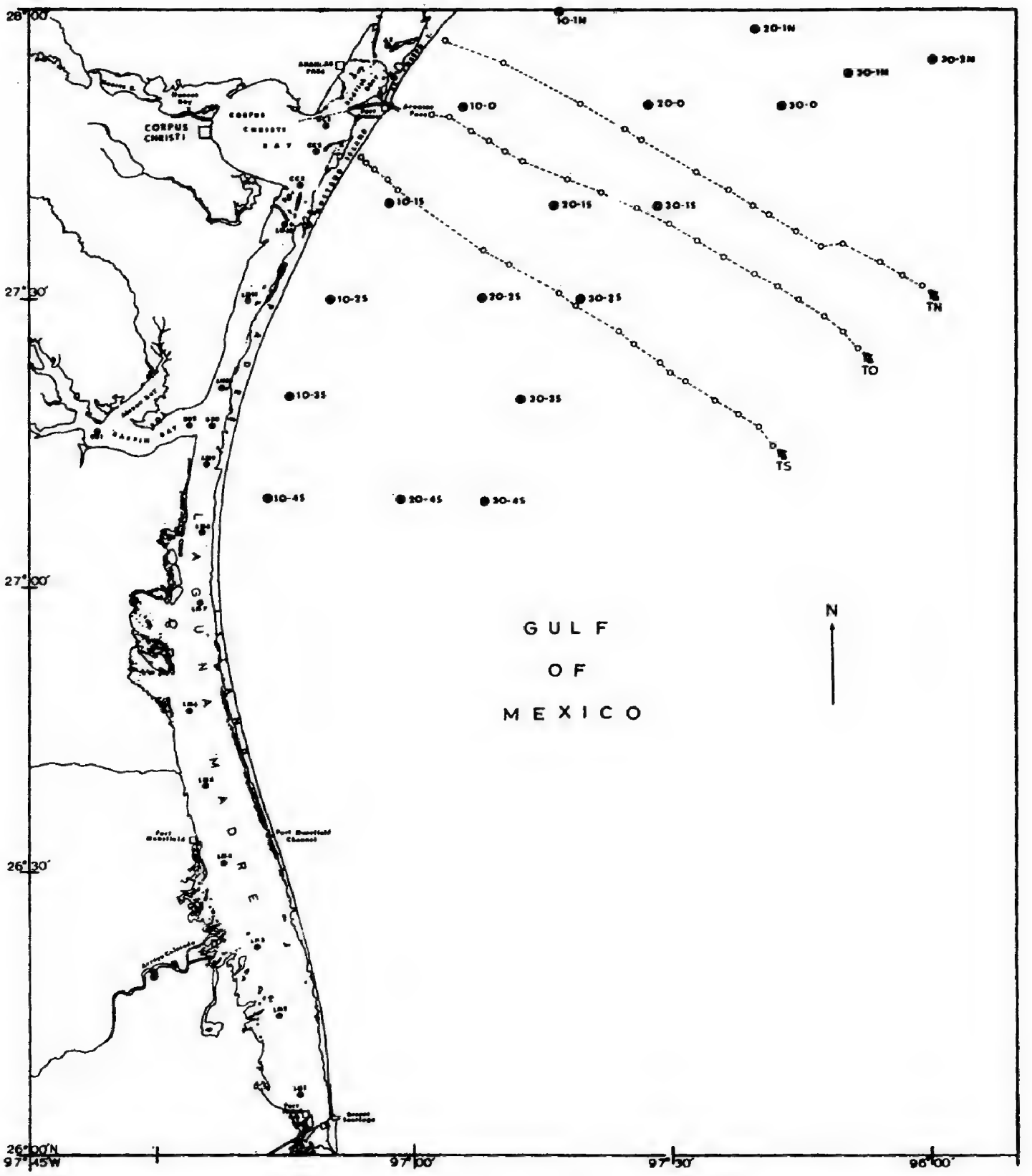

FIG. 1. Gulf of Mexico and estuarine water sampling stations—Port Isabel to Port Aransas.

through Gelman type "A" glass fiber filter pads. In comparison experiments it was found that the dissolved organic carbon (DOC) level of water so filtered was the same as that filtered through ultrafine grade fritted glass filters (Corning) with a rated pore size of 0.9–1.4 u. The glass fiber pads are more convenient to use since they are disposable and give a higher filtering rate.

Salinities were measured in the field using a temperature-compensated Goldberg refractometer (American Optical Co.). This instrument is considered accurate to within 0.5‰ of salinity (Behrens, 1965).

Clean 200 ml polyethylene bottles rinsed several times with the filtered sample were used to

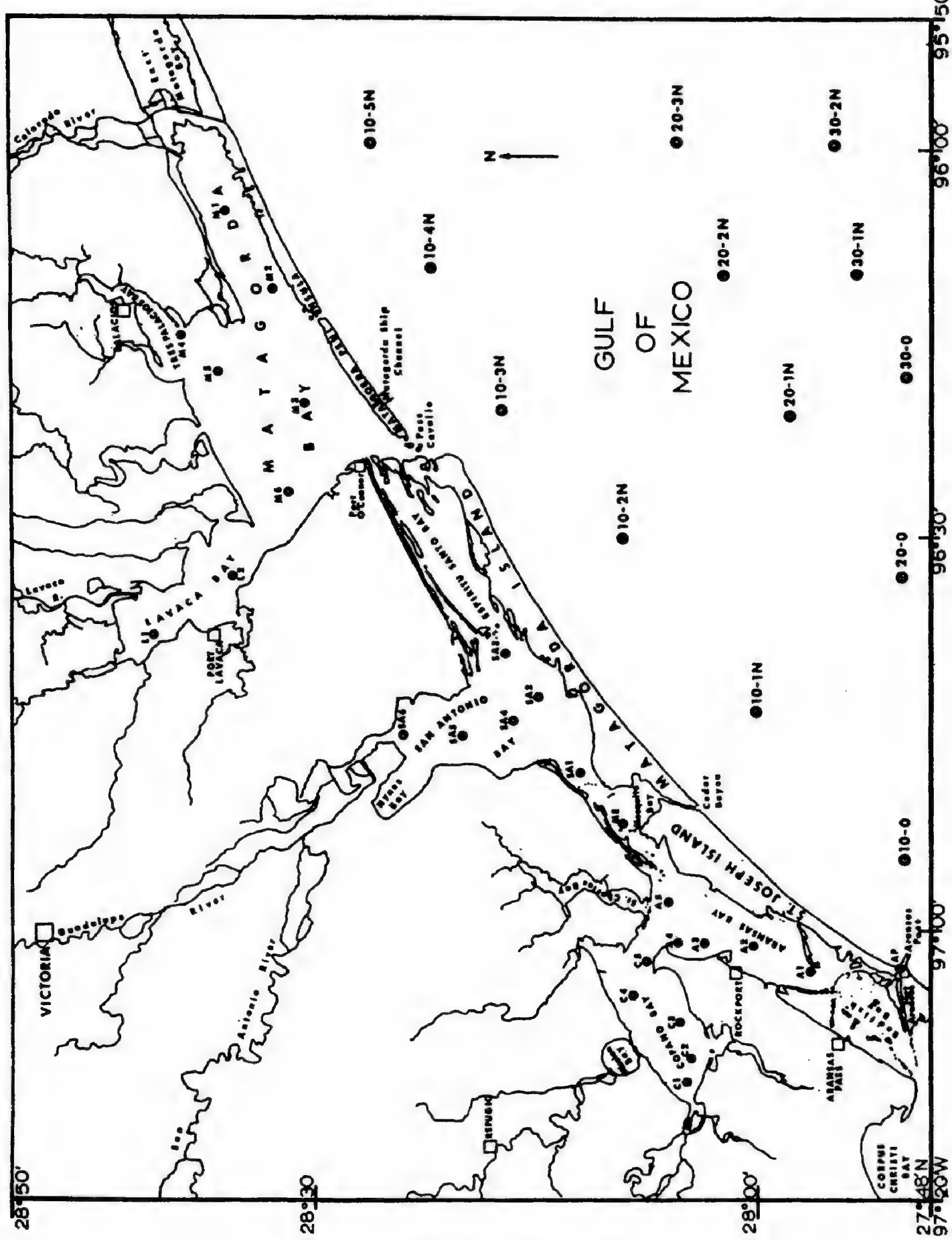

FIGURE 2

FIG. 2. Gulf of Mexico and estuarine water sampling stations—Port Aransas to the Colorado River.

store the samples. The samples were kept frozen until analyzed. No significant contamination was detected from this treatment. A sample of distilled water handled in the same fahsion showed no increase in dissolved organic carbon content.

TABLE 1

Gulf of Mexico water sampling stations parallel to the Texas coast

Station number	North latitude °	′	West longitude °	′	Collection date*
Ten fathom stations (18.3 meters):					
10–4N	28	22.5	96	08.0	6
10–3N	28	18.0	96	20.0	6
10–2N	28	10.0	96	30.0	6
10–1N	28	00.0	96	43.0	3,6
10–0	27	50.0	96	54.5	1
10–1S	27	40.0	97	03.0	1,4,5
10–2S	27	30.0	97	10.0	1,4,5
10–3S	27	20.0	97	13.5	1,4,5
10–4S	27	10.0	97	17.0	1,5
Twenty fathom stations (36.6 meters):					
20–3N	28	05.5	96	00.0	3
20–1N	27	58.0	96	20.0	3
20–0	27	50.0	96	33.5	2
20–1S	27	40.0	96	44.0	2
20–2S	27	30.0	96	52.5	5
20–4S	27	10.0	97	01.5	1,5
Thirty fathom stations (54.9 meters):					
30–2N	27	55.5	96	00.0	3
30–1N	27	54.0	96	10.0	3
30–0	27	50.0	96	18.5	2
30–1S	27	40.0	96	31.5	2
30–2S	27	30.0	96	40.5	1,3
30–3S	27	20.0	96	47.5	1,3
30–4S	27	10.0	96	52.0	1,5

* Dates: 1 = 9/24/69; 2 = 10/15/69; 3 = 11/6/69; 4 = 11/12/69; 5 = 11/21/69; 6 = 2/4/70.

TABLE 2

Gulf of Mexico water sampling stations

Distance from shore (km.) Transect TN 4/7/70	Water depth (meters)	North latitude °	′	West longitude °	′
104	183	27	31.5	96	01.5
100	165	27	32.5	96	03.5
95	139	27	34.0	96	06.0
87	126	27	36.0	96	10.0
84	110	27	36.0	96	13.0
78	91.5	27	37.0	96	16.0
72	82.5	27	38.5	96	19.0
68	73.5	27	39.5	96	21.0
63	64.0	27	41.5	96	24.0
56	55.0	27	43.5	96	27.5
44	46.0	27	46.5	96	34.0
41	37.0	27	48.0	96	35.0

30	27.5	27	50.5	96	41.0
14	18.3	27	54.5	96	50.0
1.8	9.2	27	57.0	96	56.5
Transect TS 7/1/70					
97	176	27	14.5	96	18.5
93	150	27	16.5	96	20.0
88	117	27	18.0	96	22.5
83	95.0	27	19.0	96	25.0
76	89.5	27	21.0	96	28.5
73	82.5	27	22.0	96	30.5
70	73.0	27	23.0	96	31.5
64	64.0	27	25.0	96	34.5
61	55.0	27	26.0	96	36.0
51	46.0	27	29.0	96	41.0
47	36.5	27	30.5	96	43.0
36	27.5	27	33.0	96	45.0
30	18.3	27	34.5	96	42.0
7.8	14.5	27	40.5	97	02.0
4.8	11.0	27	41.5	97	03.5
2.5	7.3	27	42.5	97	05.0
1.1	3.7	27	43.5	97	06.0
Transect TO 7/28/70					
101	175	27	25.0	96	08.5
97	152	27	27.0	96	10.5
92	135	27	28.5	96	12.5
86	113	27	30.0	96	15.5
82	102	27	31.5	96	18.0
77	91.5	27	33.0	96	20.5
70	78.5	27	35.0	96	24.5
64	68.0	27	36.5	96	27.0
58	58.5	27	38.5	96	30.5
52	51.0	27	40.0	96	34.0
44	42.0	27	41.5	96	38.0
36	35.0	27	43.0	96	42.5
28	27.5	27	44.5	96	47.5
24	24.0	27	45.5	96	50.0
20	22.0	27	46.5	96	51.5
16	20.0	27	47.5	96	53.5
12	18.3	27	49.0	96	56.0
8.3	12.8	27	49.5	96	58.0

Samples from the Laguna Madre and Corpus Christi Bay were collected similarly. Other estuarine samples were taken from the surface in a bucket and refrigerated in the polyethylene bottles and filtered on return to the laboratory, usually within 12 hours after collection. After filtering, these samples were also frozen until analyzed. Salinities were determined on the unfiltered water in the field.

(DISSOLVED ORGANIC CARBON DETERMINATION)

A modification of the persulfate method of Wilson (1961) as improved by Menzel and Vaccaro (1964) was used to measure the DOC. However a gas chromatograph was used rather than an IR detector to measure the CO_2 formed.

To convert the DOM to CO_2, 10 ml of sample was placed in a Pyrex oxidation bulb (Figure 3) with 0.4 g potassium peroxydisulfate and 0.6 ml of concentrated (85%) phosphoric acid. The

TABLE 3

Texas estuarine water sampling stations

Station number	North latitude ° ′		West longitude ° ′	
Latgune Madre 6/7/70				
LM1	26	06.0	97	13.0
LM2	26	15.0	97	16.0
LM3	26	22.0	97	19.0
LM4	26	31.0	97	23.0
LM5	26	39.0	97	25.0
LM6	26	47.0	97	27.0
LM7	26	58.5	97	26.0
LM8	27	06.0	97	26.0
LM9	27	13.0	97	24.5
BB3	27	17.0	97	24.0
LM10	27	21.0	97	22.0
LM11	27	30.0	97	20.5
LM12	27	38.0	97	15.5
Baffin Bay 5/26/70				
BB1	27	17.0	97	26.0
BB2	27	16.5	97	37.0
Corpus Christi Bay 6/7/70				
CC1	27	42.0	97	14.0
CC2	27	45.5	97	12.0
CC3	27	48.0	97	11.0
Aransas and Copano Bays 10/22/70				
A1	27	56.5	97	03.0
A2	28	00.5	97	00.5
A3	28	03.5	97	00.5
A4	28	05.5	97	00.5
A5*	28	06.0	96	57.0
C1	28	05.0	97	11.5
C2	28	04.5	97	10.0
C3	28	05.5	97	06.5
C4	28	08.5	97	05.0
C5	28	07.5	97	02.0
San Antonio-Mesquite 10/26/70				
ME	28	09.5	96	52.5
SA1	28	12.5	96	47.5
SA2	28	15.0	96	42.0
SA3	28	17.0	96	39.0
SA4	28	16.5	96	44.0
SA5	28	20.0	96	45.0
SA6	28	24.0	96	45.0
Matagorda-Lavaca 10/30/70				
M1	28	36.0	96	05.5
M2	28	32.5	96	11.0
M3	28	30.5	96	20.5
M4	28	39.5	96	14.5
M5	28	36.5	96	17.5
M6	28	31.5	96	26.5
LA1	28	35.5	96	33.5
LA2	28	41.0	96	37.5

* Taken with Mesquite-San Antonio samples on 10/26/70.

FIGURE 3

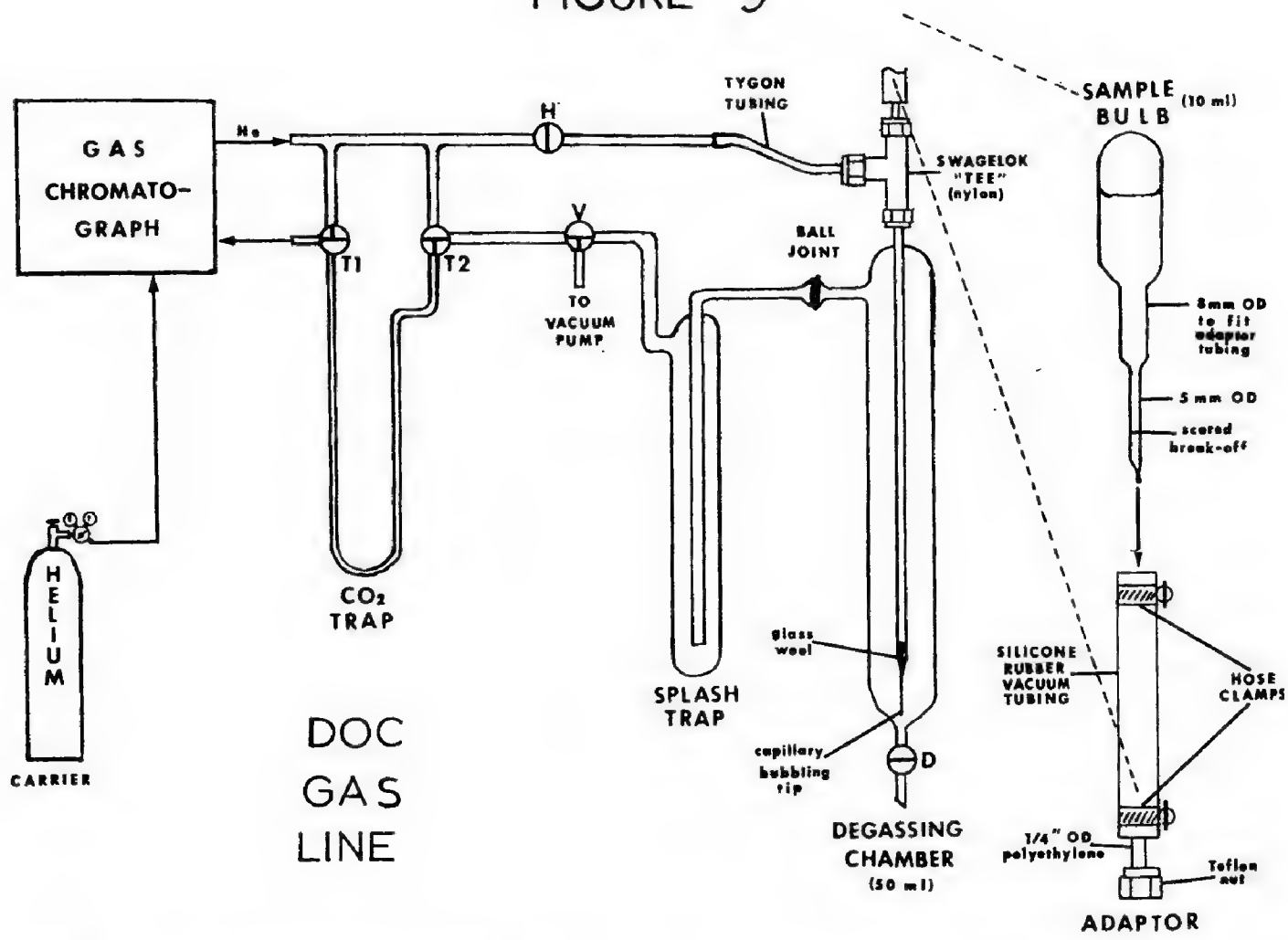

FIG. 3. Dissolved organic carbon (DOC) analysis apparatus. Stopcocks are shown as set for evacuation (see text). D is a drain cock used to empty the degassing chamber after each sample.

sample still contained dissolved CO_2 from the bicarbonate in the water and so it was then sparged with nitrogen for two minutes through a 20 gauge hypodermic needle. The bulbs were then sealed under partial vacuum (water asirator). Light tapping on the bottom of the bulb with a stiff piece of cardboard while sealing was found to aid in the release of dissolved gases.

The samples were then oxidized in an autoclave at 125°C for an hour. The CO_2 formed was measured with the apparatus diagrammed in Figure 4. This apparatus will be referred to as the "gas line." An Aerograph 202 Gas Chromatograph (Varian Associates) was used with a 6 ft. x 0.25 in. (OD) copper column packed with Poropak Q (Waters Associates) and helium carrier in a 50°C oven. Inlet pressure was 20 lbs., analytical column flow was 45 ml/min and reference flow (open tubular, 0.125 in. OD) was about 20 ml/min. Detection was by a thermal conductivity bridge operated at 175 ma.

The following steps, along with Figure 4, outline the procedure used for measuring the CO_2 formed from the oxidation:

1. Sealed off tip of bulb scored on opposing sides with a glass knife to aid breaking open.
2. Sample bulb inserted into adaptor and hose clamp finger-tightened to prevent leakage.
3. If sample contained visible chlorine which could form by oxidation in samples containing chloride ion, 5 ml of 20% potassium iodide in 10% sulfuric acid was introduced into the degassing chamber.
4. With H closed and T1 set to bypass carrier flow directly into the gas chromatograph, the bulb and adaptor were screwed finger tight onto the swagelok inlet of the degassing chamber and the entire gas line evacuated through V.
5. With V set back to the flow-through position a liquid nitrogen bath was placed around the CO_2 trap and the break-off snapped by flexing the adaptor tubing. The liquid and gases from the bulb then flowed into the degassing chamber and most of the CO_2 diffused into the trap and condensed.

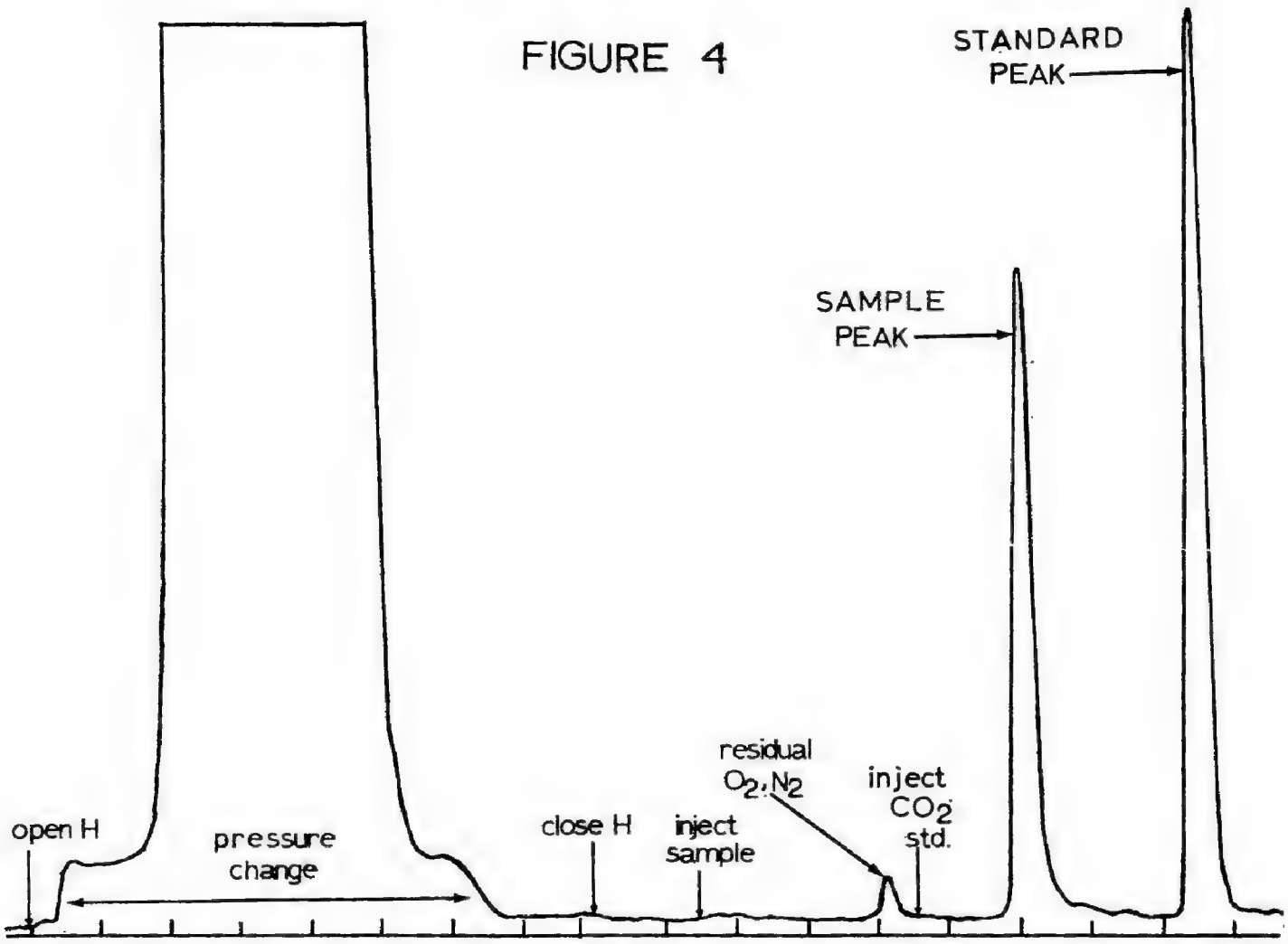

FIG. 4. Typical analytical trace for a DOC measurement. Lower scale is marked at half-minute intervals.

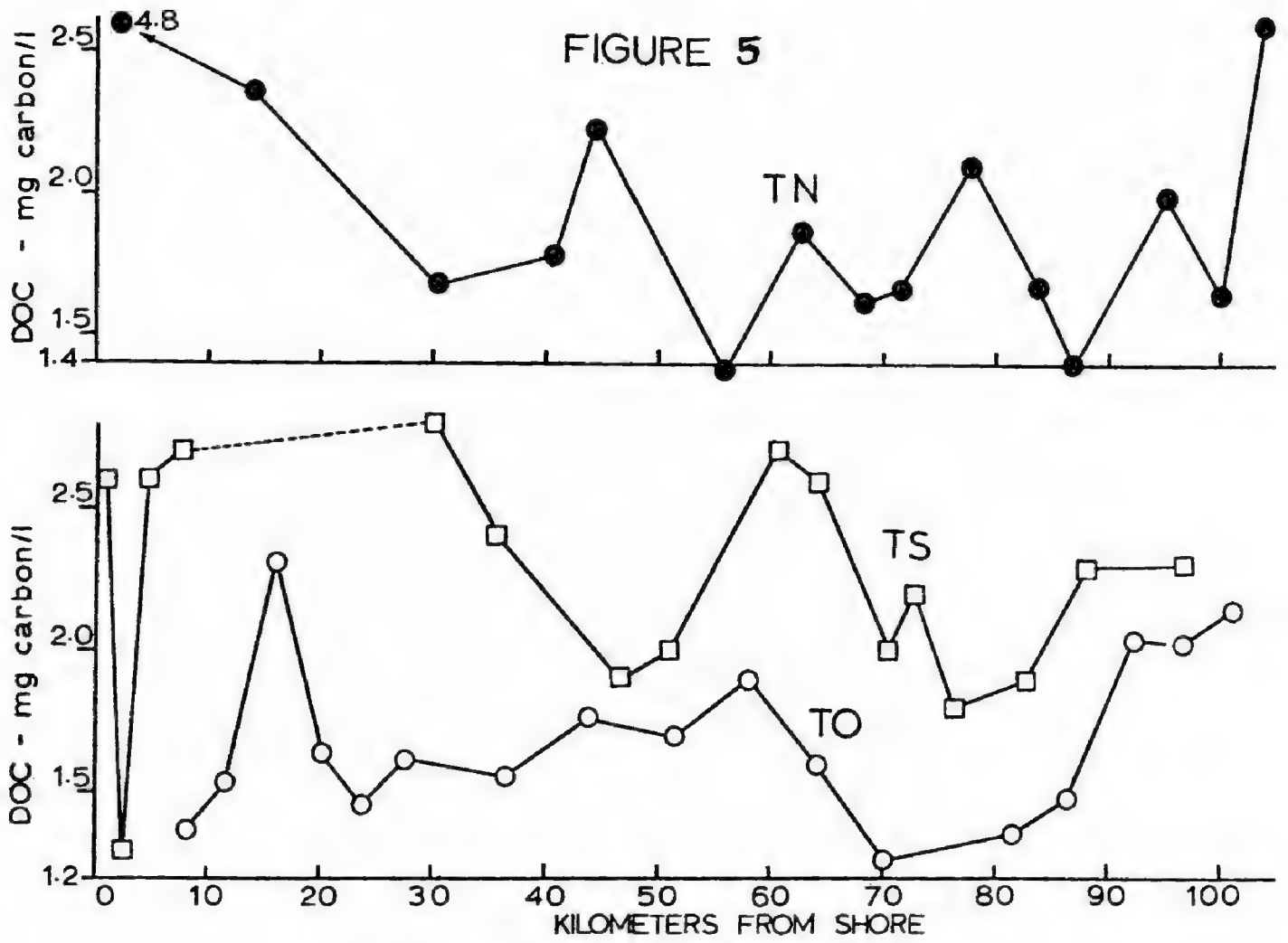

FIG. 5. DOC values for Gulf of Mexico transects.

6. After bubbling from the capillary tip ceased, H was opened and carrier gas allowed to flow in to bring the gas line pressure back up, and to sweep the remaining CO_2 into the trap. Repressurization took about four minutes and was indicated when the recorder trace returned to the baseline (Figure 4).
7. Leaving the liquid nitrogen in place, excess gas was evacuated from the CO_2 trap *only* by *momentarily* opening it to the vacuum. This eliminates O_2 and N_2 liberated in the oxidation which would otherwise give a large peak that could overlap the CO_2 peak.
8. After closing all ports of T2 with a 45° turn, the liquid nitrogen was replaced by an *iso*propanol-dry ice slurry which allowed the CO_2 to vaporize for injection into the chromatograph while keeping interfering water and iodine vapors frozen. Originally, a slurry was also kept on the splash trap, but was later found to be unnecessary.
9. Allowing about 30 seconds for the CO_2 to vaporize, T1 and T2 were reset to divert the carrier flow through the trap sweeping its gaseous contents onto the analytical column. When the residual air had eluted (Figure 5) a standard volume of CO_2 was injected directly into the analytical column for calibration and then T1 and T2 were set back and the line was ready for the next sample.

(STANDARDS)

Several types of standards were used to check the reliability of various parts of the analytical procedure.

The actual amount of CO_2 eluted from the column was determined by comparison of peak areas to those of known amounts of CO_2 injected through the sample ports of the chromatograph. Areas were computed as the product of the peak height and peak width at half-height.

The efficiency of gas recovery from the gas line was checked first by injecting known concentrations of CO_2 in air into the evacuated gas line through a septum on the inlet, and secondly, by injecting known amounts of a standard sodium carbonate solution followed by 5 ml of 10% phosphoric acid. An average of 93% of the injected CO_2 was recovered while 95 to 99% of carbonate CO_2 was recovered.

Various compounds in water solution were tested to check the efficiency of the oxidation and recovery from samples. Table 4 summarizes these tests. Similar checks on known compounds have been performed by Wilson (1963) and Williams (1969).

(BLANKS)

Since sea water contains nearly 30 times as much bicarbonate carbon as organic carbon, the procedure was carried out through the sealing step on bicarbonate solutions to prove that all inorganic carbon was being moved before oxidation. In all cases no detectable CO_2 was recovered from the bicarbonate.

The KI solution alone in the gas line gave no recoverable CO_2 as would be expected from an acidic solution. Our distilled water supply was found to contain from 1 to 5 mg C/l unless collected fresh from the still head (Bellco-glass), where it still yielded about 0.3 mg/l. So to

TABLE 4

Efficiency of persulfate oxidation with known compounds

Compound	Mean percent of carbon recovered
Potassium acid phthalate	98
Lactose	97
Starch	104
Guanosine	87
Bovine serum albumin*	95

* Assuming 45% carbon as a typical protein. (White *et al.*, 1964).

check the reagent blank, a large volume of distilled water was autoclaved with persulfate and acid to oxidize all its organic matter. This water was then used as a blank and as a dilutant for particularly concentrated samples. Reagent blanks determined in this way averaged 0.66 mg C/l with a standard devviation of 0.12 mg C/l.

The reagent blank was also determined by oxidizing different volumes of filtered Aransas Pass water, and plotting a regression to zero volume. The blank from this method was 0.46 mg C/l. (All chemicals used were reagent grade.)

Triplicate determinations generally agreed within 0.2 mg C/l except for very high organic concentrations (20 mg C/l) which never varied more than 5%.

RESULTS AND DISCUSSION

The close sampling of the Gulf of Mexico continental shelf area near Port Aransas supports previous work and also revealed details of the near-shore DOC distribution not found by earlier workers.

Figure 5 shows DOC concentrations on the TN, TO and TS transects. The most striking feature of the data is the occurrence of maxima and minima. It has generally been assumed that DOC levels steadily decline with distance from shore (Fredericks and Sackett, 1970). The strong similarities between the TO and TS curves, taken one month apart, suggests the persistence of these zones. Even the TN data taken three months earlier give the same shaped curve although the highs and lows are displaced. Szekielda (1969a, b) has noted a similar phenomenon with POM near the east African coast, and proposes a circulation cell model to account for it. He mentions that photographs of the Laguna de Terminos and Campeche Bay areas of the Gulf coast taken by the Gemini V astronauts reveal alternating light and dark. We have noted streaks of differing colors in the water on sampling cruises which may have been the same phenomenon, but no significance was attached to them at the time so they were not recorded for possible correlation. The dark or clear areas are supposedly areas of convergence (downwelling) while the light or turbid areas represent divergence (upwelling). We hope to be able to examine possible seasonal changes of this banding in the future.

As an aid in assessing any estuarine effects on nearshore waters, DOC's and salinities were measured for the Texas coastal lagoon system from the Rio Grande to the Colorado River. The general trends of these values are shown in Figures 6, 7, 8 and 9.

Baffin Bay and the adjacent laguna are in an area of minimal fresh water run-off and tidal exchange. Evaporation usually outweighs either of these factors so the system tends to hypersalinity except when flushed out occasionally by heavy rains and run-off, which accompany tropical storms. Hurricane Beulah in the summer of 1967, and unusually heavy rains the following year effectively reduced the bay to zero salinity. By March, 1969, salinity had returned to 30‰ and when last sampled in December, 1970, was already at 47‰.

The high DOC must be in part due to its concentration by evaporation, but there is not a direct proportionality to the salinity as would be expected of a conservative component. There must be other effects such as changes in plankton population and productivity accompanying the salinity change (Wilson, 1963).

FIGURE 6

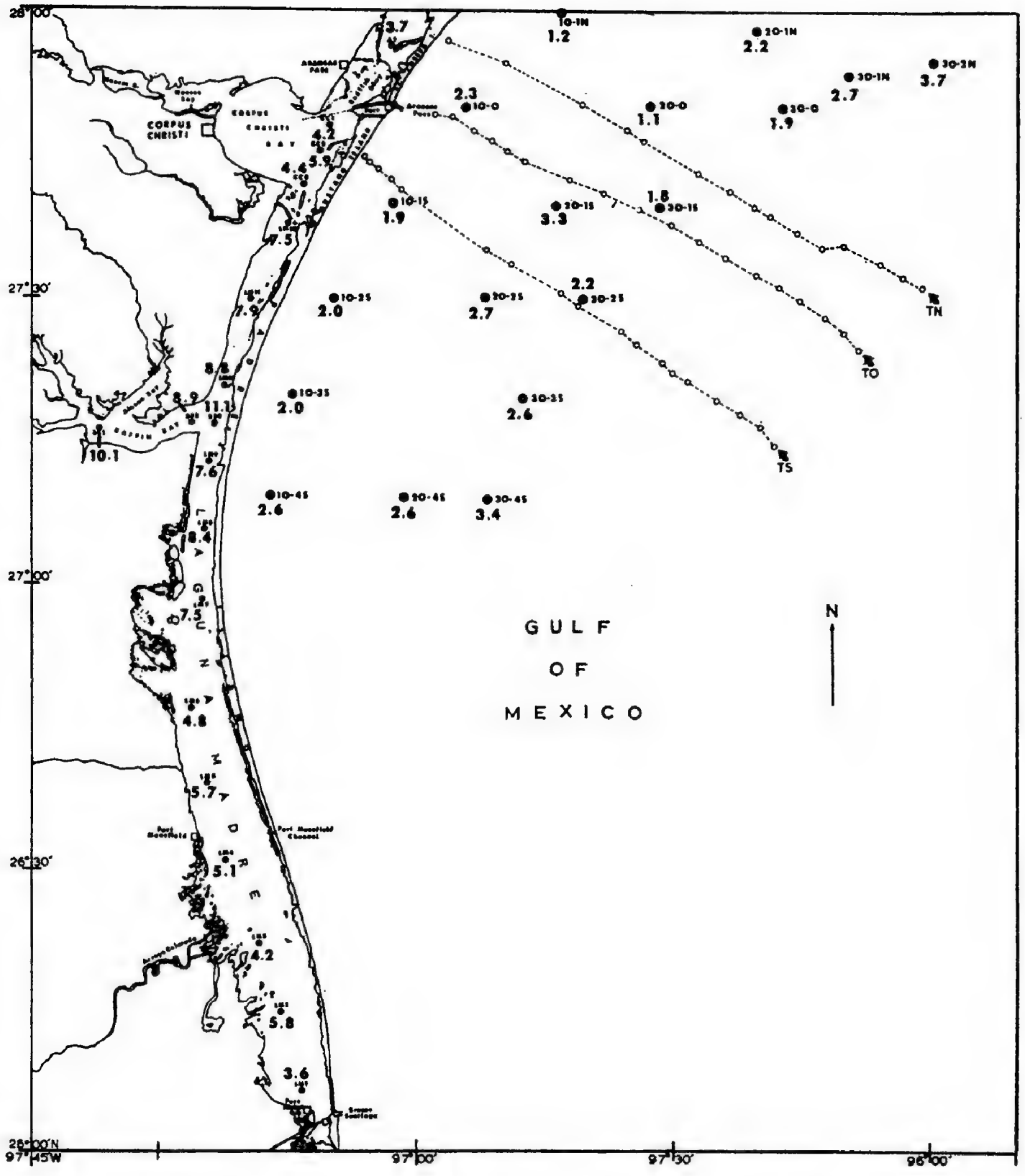

FIG. 6. DOC values in mg carbon/liter for Gulf of Mexico and estuarine samples from Port Isabel to Port Aransas. For TO, TN and TS transect values, see Figure 5. Smaller letters and numbers are station designations (see also Tables 1–3) while larger numbers are DOC values.

The changes in DOC in Baffin Bay after the hurricane as reported by Calder (1969) also reflect this non-proportionality.

The lower DOC values in the extreme south and northern half of the system are as expected since these are areas of exchange with Gulf water which generally has a lower amount of organic carbon (Figures 8 and 9). The minimum vaules near Aransas Pass and Cedar Bayou especially show the Gulf influence.

FIGURE 7

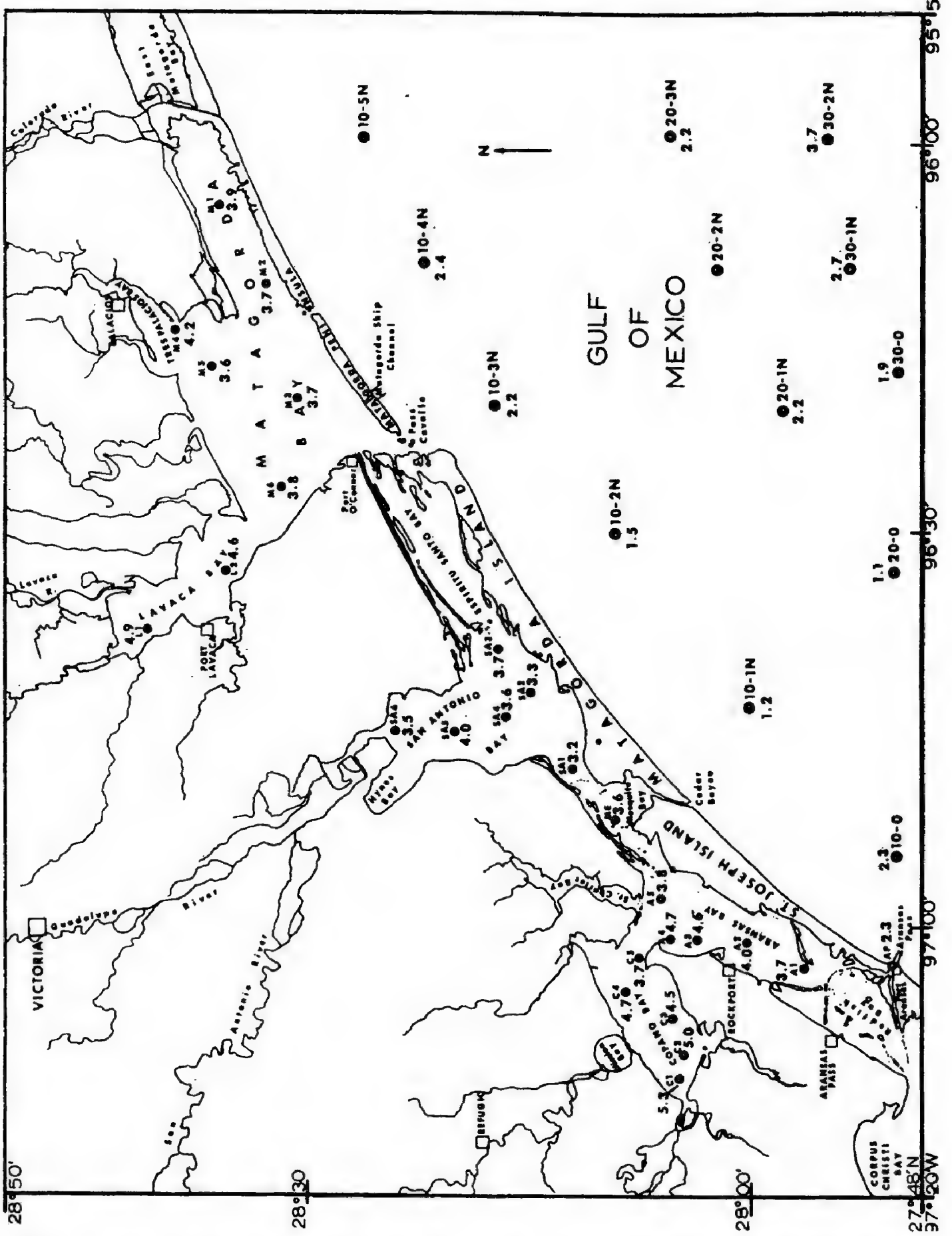

FIG. 7. DOC values (mg carbon/liter) for Gulf of Mexico and estuarine samples from Port Aransas to the Colorado River. Numbering and lettering have same significance as Figure 6.

The individual estuaries comprising this system were separately examined to assess their particular contributions to the DOC patterns. An inverse relationship between DOC and salinity in areas of fresh and salt water mixing was noted

FIGURE 8

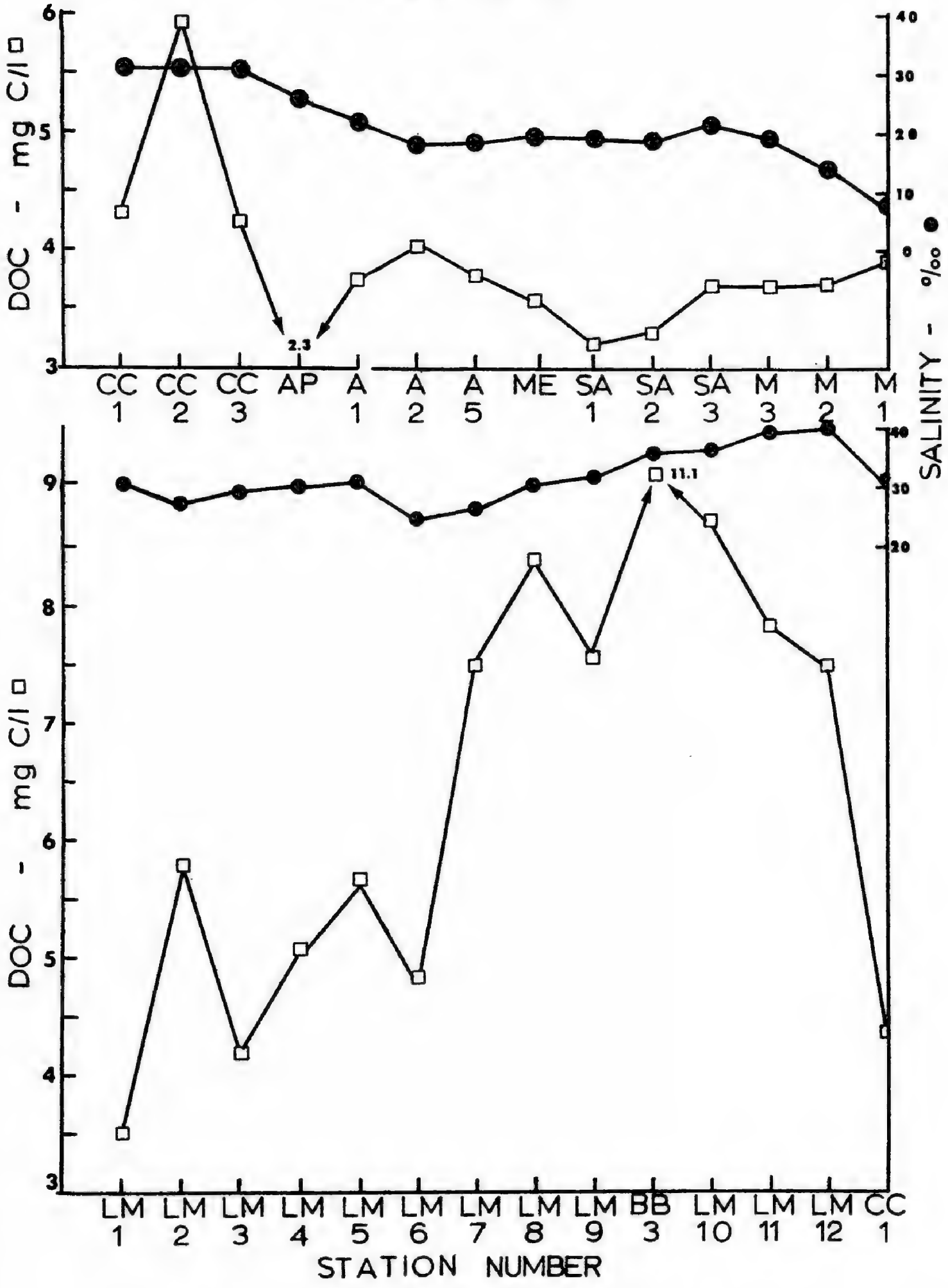

FIG. 8. DOC and salinity values for laguna stations from Port Isabel to the Colorado River. See Figures 6 and 7, and Tables 1–3 for station locations.

FIGURE 9

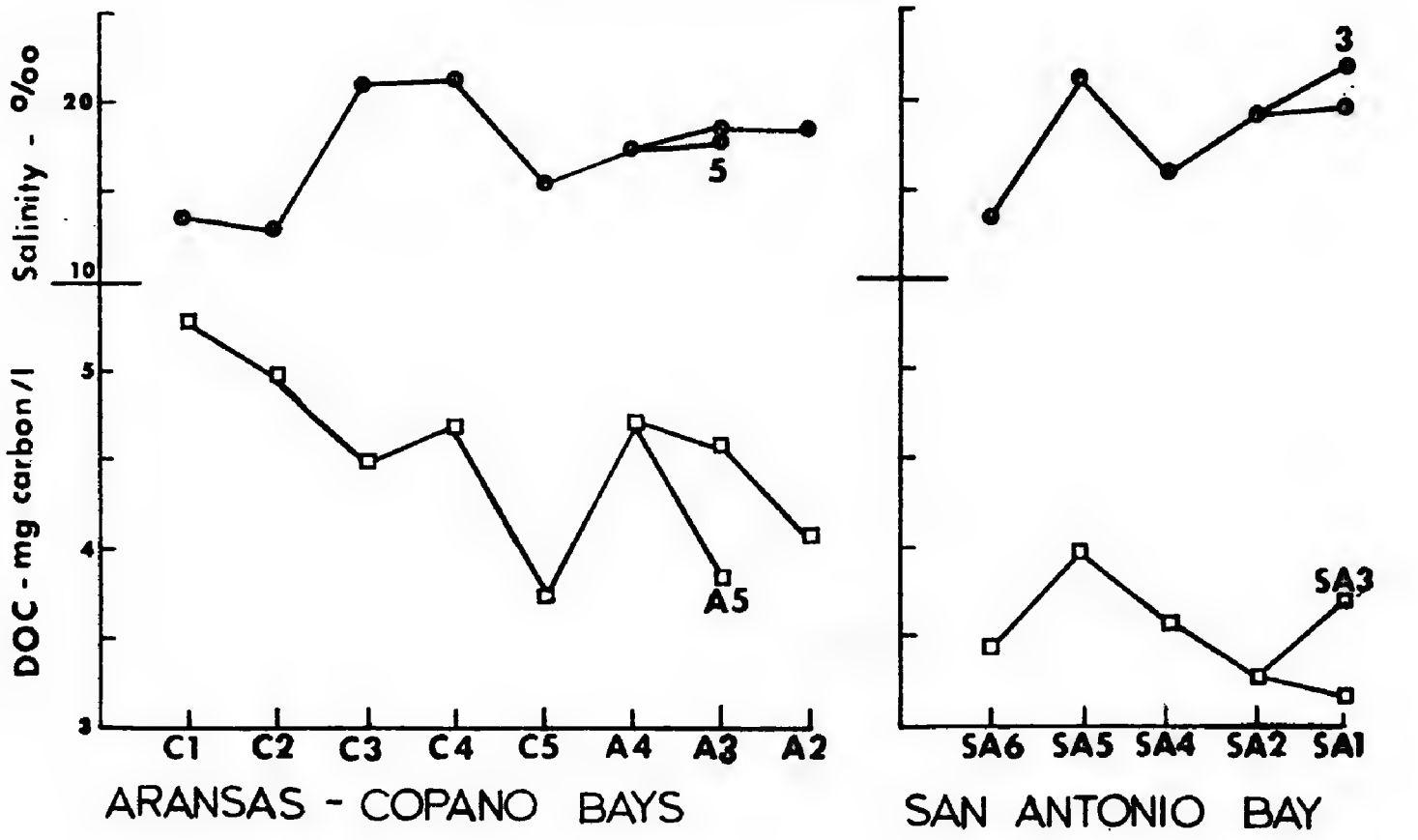

FIG. 9. DOC and salinity values for Texas estuary stations from Port Aransas to the Colorado River. See Figure 7 and Tables 1–3 for locations.

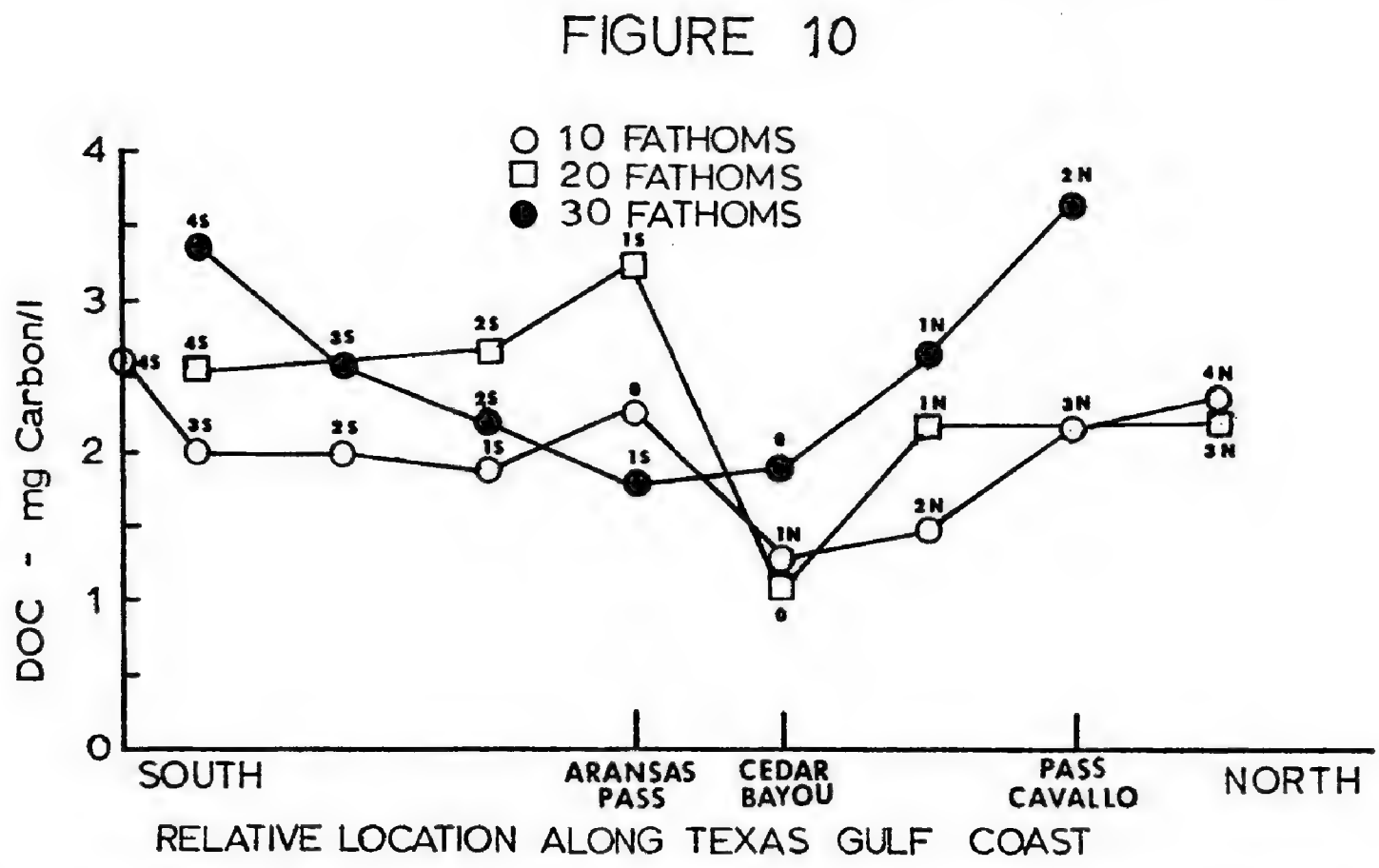

FIG. 10. DOC values for transects parallel to the Texas Gulf of Mexico coast. Designations above each point correspond to those in Figures 6 and 7.

(Figure 9). The same situation has been found by Fredericks and Sackett (1970), where the Brazos and Mississippi Rivers enter the Gulf of Mexico. This suggests the higher DOC of river water is being diluted by the less rich marine waters. In any case, it is apparent that the effects of fresh water inflow do not extend very much toward the seaward end of the bays, and consequently would not be expected to have much influence on the Gulf DOM except very near shore.

This seems to hold for the transects parallel to the coastline (Figures 6, 7 and 10) with maxima near the areas of exchange at Aransas Pass and Pass Cavallo on the 10 and 20 fathom lines. The changes in the 30 fathom values are probably due to *in situ* effects and do not reflect any influence of estuarine waters. A curious but unexplained observation is the coincidence of the minima on all transects even though they are adjacent to the maxima on the 10 and 20 fathom lines.

Note that the three curves cross each other at several points showing again the zonation of DOC, since a smooth decrease with distance from shore would give nearly parallel curves. More closely spaced sampling on these parallel transects might have revealed more of the pattern of estuarine influence on the DOC.

Wilson (1963) has measured total organic carbon (dissolved plus particulate) in the same estuaries reported here. His values were mostly higher than reported here, in part due to the high amounts of particulate matter in these waters. Also, his samples were taken during a period of drought when evaporation may have increased the DOC. Steed (1971) made a detailed study of the organic carbon in the Guadalupe-San Antonio estuary wherein he found DOC levels similar to those reported here. He found particulate carbon concentrations to be approximately equal to dissolved.

The variations in DOC levels found for these shelf waters suggest that near-shore DOC unlike deep sea DOC (Menzel & Ryther, 1970) is closely coupled to the biological carbon cycle. The gradual transport of this near-shore material, to the deeper waters of the Gulf is being investigated in our laboratory.

ACKNOWLEDGMENTS

Acknowledgment is made to the donors of The Petroleum Research Fund, administered by the American Chemical Society, for support of this research (PRF Grant 4158-AC2).

LITERATURE CITED

BEHRENS, E. W. 1965. Use of Goldberg refractometer as a salinometer for biological and geological field work. *J. mar. Res.* **23:** 165–171.

CALDER, J. A. 1969. Carbon Isotope Effects in Biochemical and Geochemical Systems. *Ph.D. Thesis. Univ. of Texas*, Austin.

FREDERICKS, A. D. and W. M. SACKETT. 1970. Organic carbon in the Gulf of Mexico. *J. geophys. Res.* **75:** 2199–2206.

MENZEL, D. W. and R. F. VACCARO. 1964. The measurement of dissolved and particulate organic carbon in the sea. *Limnol. Oceanogr.* **9:** 138–142.

MENZEL, D. W. and J. H. RYTHER. 1970. Distribution and cycling of organic matter in the oceans, p. 31–54. In D. W. Hood (ed) *Symposium on Organic Matter in Natural Waters.* University of Alaska, College.

STEED, D. L. 1971. Some aspects of organic carbon transport in Guadalupe-San Antonio Estuary, Texas. *Ph.D. Thesis. Univ. of Texas,* Austin.

SZEKIELDA, K-H. 1969a. La repartition du material organique devant les cotes. *C. r. hebd. Seanc. Acad. Sci., Paris.* **268:** 2323–2326.

SZEKIELDA, K-H. 1969b. Der Einfluss vertikaler Bewegungsvorgange auf die Konzentration organizchen Materials in Zirkulationszellen voe Kusten. *Geochim. cosmochim. Acta.* **33:** 1233–1246.

WILLIAMS, P. J. LEB. 1969. The wet oxidation of organic matter in sea water. *Limnol. Oceanogr.* **14:** 292–297.

WILSON, R. R. 1961. The measurement of organic carbon in sea water. *Limnol. Oceanogr.* **6:** 259–261.

WILSON, R. F. 1963. Organic carbon levels in some aquatic ecosystems. *Publs Inst. mar. Sci. Univ. Tex.* **9:** 64–76.

SIZE-RELATED METABOLIC RESPONSES OF THE PINFISH, *LAGODON RHOMBOIDES*, TO SALINITY VARIATIONS AND SUBLETHAL PETROCHEMICAL POLLUTION[1]

Thomas C. Kloth[2] and Donald E. Wohlschlag

The University of Texas Marine Science Institute, Port Aransas, Texas 78373

ABSTRACT

The effects of salinity variations on the respiratory metabolism of large and small pinfish, *Lagodon rhomboides*, in unpolluted water and in water slightly polluted with a 0.5% petrochemical effluent were investigated at near-saturation dissolved oxygen levels and at a near-optimum temperature of 20°C.

A salinity range of 20–45 ppt did not significantly affect the respiratory metabolism of large or small pinfish in unpolluted water. However, sustained swimming velocities were affected by salinity. The highest sustained swimming velocities were found at 20 ppt, for both large and small pinfish, and the velocities decreased as salinity increased. Sustained swimming velocities of large pinfish decreased more than those of small pinfish.

Sublethal pollution uniformly depressed small fish metabolism at all salinities. With large pinfish, pollution depressed metabolism at 20 and 32 ppt, but elevated metabolism at 45 ppt. Multiple regression analysis showed that salinity had a statistically significant effect on respiration only with large pinfish in polluted water.

INTRODUCTION

The purpose of this study is to establish and evaluate levels of respiratory metabolism of the pinfish in two body size ranges, over a range of salinities, at a constant temperature, and with or without a very low, sublethal level of a pollutant.

Several studies have indicated that the size of a pinfish influences its reaction to such variables as temperature and sublethal pollution. Wohlschlag and Cameron ,1967) have shown that sublethal pollution affects the respiration of large pinfish more than that of small pinfish, especially at high and low temperatures. Likewise, larger pinfish appear to be affected more than small pinfish by thermal stress (Wohlschlag *et al.*, 1968; Wohlschlag and Cech, 1970). Cameron (1969) found that larger pinfish tend to move off shallow grass flats sooner than smaller pinfish during diurnal and seasonal high temperature extremes.

[1] Modified from a thesis presented by the first author to the Graduate School, The University of Texas, in partial fulfillment of the requirements for the degree of Master of Arts, August, 1970.

[2] Present address: The Dow Chemical Company, Texas Division, Freeport, Texas 77541.

The general effects of salinity variations on energy requirements of coastal fishes have both theoretical and pragmatic implications in explaining both distributional and abundance patterns and growth and productivity levels. Few species can thrive continuously in a given coastal locality over either regular or sporadic, but broadly varying, salinities brought about by natural fluctuations due to tides, floods and droughts. Additional upward fluctuations in salinities in coastal areas are more and more frequently due to man-made freshwater diversions of fresh water; the average increasing salinities in such cases can be relieved only relatively more sporadically by occasional severe floods as freshwater diversions increase. Some species can tolerate given salinity conditions during only specific portions of their life cycles and must depend upon either "directed" or random migratory movements to occupy successfully a given coastal locality at propitious periods of their life cycles.

The effects of salinity on fish respiration are not well understood and apparently often have been underestimated until recently. Gunter (1961) noted that Alee *et al.*, (1949) concluded in their book *Principles of Animal Ecology*, that salinity was not ordinarily an important limiting factor for animal populations. Kinne (1964) has given an extensive review of the effects of salinity on various marine organisms including fish and believes salinity and temperature to be ecological master factors. Parry (1966) has reviewed omsotic and ionic organization of different groups of fish in relation to their environments. Patterns of osmoregulation in marine and freshwater fishes are reviewed by Umminger (1971) with special reference to temperature. A number of studies have found metabolic responses to salinity to be size dependent, although the responses may not form a generalized pattern for all species (Keys, 1931; Wohlschlag, 1957; Hickman, 1959, Job, 1959, 1969; Parvatheswararao, 1965; Subramanian, 1967).

The combined effect of salinity and pollution on fish has received little attention. Eisler (1965) found that salinity affected the toxicity of synthetic detergent concentrations on the mummichog, *Fundulus heteroclitus*. The natural salinities of the waters along the entire Gulf coast range from brackish to hypersaline, and petrochemical effluents are discharged variously throughout the entire coastal region (Copeland and Wohlschlag, 1968). It is therefore important to assess the biological significance of the effect of salinity with and without petrochemical effluents.

Even though ranges of oxygen consumption as indicators of total metabolism may vary widely for some fishes, there appears to be a rationale for explaining either upward (loading) or downward (limiting or inhibiting) perturbations in total metabolism due to sublethal stress (Brett, 1958). For the case of total metabolism, Kerr (1971) indicates that major components are the energy of foraging activity, the cost of standard metabolism, the energy cost specific to utilization of food, and the energy expended upon spontaneous activity. At optimum conditions of temperature pertinent to a given species, an increasing body of data appears to indicate that there is optimal food utilization and growth (Brett, 1971). Kinne (1964) indicates that the same optimal biological situation for both temperature and salinity tend to prevail for a variety of organisms. At less than optimal conditions, e.g. with sublethal pollution, there is a tendency for

total metabolism to be reduced, as illustrated by a maximum depression in the pinfish at low temperatures, moderate depression at high temperatures and a minimum depression at an intermediate, near-optimum temperature (Wohlschlag and Cameron, 1967). In cases of metabolic depression, it is conceivable that any or all of Kerr's (1971) four components of total metabolism would be reduced, although Brett's (1971, Table 1) interpretation indicates that standard metabolism costs would have to be maintained at a given temperature, regardless of stress effects on other functions. On the other hand, under some conditions of sublethal stress, it is conceivable that the effects would be to increase the "normal" total metabolism by a "loading" increase from spontaneous activity, the cost of swimming activity, the cost of utilization of food, or a combination of these energy requirements. One of the obvious consequences of continuous, slight loading due to sublethal stress would be a reduced growth rate, other conditions being equal. Similarly slight sublethal stresses would tend to decrease swimming propensities, unless more energy than normally available would be expended, in which case an oxygen debt could result. Brett (1971, Table 1) summarizes some of these situations with respect to temperature.

Thus in some natural environmental situations over a range of temperature and salinity variables, it would be logical that near the extremes of either or both of these variables, total metabolism could be either raised or lowered when an additional sublethal stress is applied.

In this study, respiration rate is oxygen consumption per hour, and metabolic rate is oxygen consumption rate per unit weight.

MATERIALS AND METHODS

Experiments were performed from April to June, 1970, at Port Aransas, Texas. Pinfish were obtained either by traps or hook-and-line in the Aransas Pass near the Gulf of Mexico. The fish ranged in weight from 17 to 292 gm and were arbitrarily designated as large or small. "Large" pinfish weigh more than 70 gm while "small" pinfish weigh less than 70 gm.

Normal seawater (30–35 ppt) was obtained from either settling ponds or from the Aransas Pass on an inflowing tide. Low salinity water (20 ppt) was made by mixing normal seawater with city tap water, followed by aeration for several days prior to use to remove chlorine. Hypersaline seawater (45 ppt) was obtained by allowing normal seawater to evaporate outdoors until the desired salinity was reached. Salinity was measured with a Goldberg refractometer.

Pinfish were caught at a salinity of 30–35 ppt and immediately transferred to either the low salinity water or hypersaline water for an acclimation period of at least two weeks. The fish for the normal salinity (30–34 ppt) experiments were merely placed in 463-liter aquaria for temperature acclimation. Seven to ten experiments were conducted with each set of conditions for both large and small fish.

A petrochemical effluent from a refinery in Corpus Christi, Texas was used for the pollution experiments. Mr. Roy Spears of the Texas Parks and Wildlife Department provided the effluent analysis using standard methods. Fish were acclimated to the polluted water for two days before experimentation began.

Experiments were conducted in two 463-liter insulated aquariums. The aquarium water was kept at approximately 20°C and was continuously aerated to eliminate the effects of low dissolved oxygen concentration on respiration.

If the ambient water temperature were in the 15–25°C range, the pinfish were held for two or three days at 20°C before experiments were conducted. If the ambient water temperature were more than 25°C, the fish were first held at 25°C for two days. Over an eight-hour period, the temperature was lowered to 20°C and the fish were again held for two or three days at 20°C.

Two enclosed plastic, circular chambers were used to determine the respiratory metabolism. Large fish were placed in a 42,140-ml chamber while small fish were placed in a 9,500-ml chamber. The fish were allowed to acclimate to the chamber for one hour before the experiments began. The chambers were suspended in the 463-liter insulated aquariums and rotated at whatever speed a fish would maintain over a 45-minute period. The swimming track of the large chamber was about two meters per revolution, while the swimming track of the small chamber was approximately one meter per revolution.

Water samples of 280-ml were taken initially and at three, successive 15-minute intervals. The dissolved oxygen concentration of these samples was determined using the Winkler method with the azide modification (Carrit and Carpenter, 1967). A linear regression through the four points was calculated to determine the rate of oxygen consumption in mgO_2 per hour. Blank runs without fish were made to correct for any oxygen consumption by small organisms or chemical systems in the water. After each run, the weight and length of the fish was recorded along with the number of revolutions of the chamber. Multiple regression analysis followed the form given by Wohlschlag and Cameron (1967). The oxygen consumption rate may be related to several independent variables in the form:

$$Y = a + b_w X_w + b_v X_v + b_s X_s$$

Y is the expected log mgO_2 consumed per hour,
a is a constant,
b_w is a partial regression coefficient of the increase in Y per unit increase in log weight at constant salinity and swimming velocity,
x_w is the log weight in grams,
b_v is the partial regression coefficient of the increase in Y for each m/min. increase in swimming velocity at constant salinity and weight,
x_v is the average swimming velocity in m/min.,
b_s is the partial regression coefficient of the increase in Y for each unit increase in salinity at constant weight and swimming velocity, and
x_s is salinity in ppt.

RESULTS

An analysis of the petrochemical effluent used in this study is given in Table 1. Table 2. contains the average respiratory data with multiple regression equations and statistics in Tables 3 and 4, respectively. The multiple regression equations in this study are used primarily to calculate comparative oxygen consumption rates at specific body weights, salinities, and swimming velocities to facilitate evaluation of metabolic trends.

TABLE 1

Analysis of the petrochemical effluent

Constituent	Concentration (mg/l)
Sulfates	320
Iron	0.3
"p" alkalinity	50
Total alkalanity	327
Chlorides	745
Suspended solids	40
Total residue	1298
Sulfides	25
pH	8.6

TABLE 2

Average respiration data
(see Tables 3 and 4 for regressions and regression statistics)

Fish size	Water condition	Salinity ppt	Number of observations	Ave. wt. gm.	Ave. RR*	Ave. MR†	Ave. SV‡ m/min	Ave. SV§ bl/min
Large	Unpolluted	20.8	10	127	54.8	434.7	22.30	131.2
Large	Polluted	20.8	10	177	36.2	216.7	16.10	89.9
Small	Unpolluted	19.7	10	42	19.0	457.6	11.92	107.4
Small	Polluted	19.7	9	36	12.5	441.8	10.93	105.1
Large	Unpolluted	30.2	10	144	54.9	371.0	13.62	83.6
Large	Polluted	30.7	10	168	64.8	392.6	12.47	70.9
Small	Unpolluted	32.9	7	52	22.1	445.5	8.98	75.5
Small	Polluted	34.0	10	43	15.3	354.1	5.26	49.6
Large	Unpolluted	45.6	7	133	47.0	365.6	8.64	54.3
Large	Polluted	44.5	7	163	60.7	360.3	9.46	56.3
Small	Unpolluted	45.6	7	54	20.4	384.9	8.92	75.0
Small	Polluted	47.2	10	52	23.9	464.2	9.03	74.6

* Respiration rate, mgO_2/Hr.
† Metabolic rate, $mgO_2/Hr/Kg$.
‡ Swimming velocity, m/min.
§ Swimming velocity, body lengths/min.

TABLE 3

Multiple regression equations

		N	
(1)	L–U: 20–45 ppt†	27	$Y = -0.4791 + 1.0104X_w + 0.0038X_v - 0.0008X_s$
*(2)	S–U: 20–45 ppt	24	$Y = 0.9272 + 0.2703X_w + 0.0004X_v + 0.0005X_s$
(3)	L–P: 20–45 ppt	27	$Y = -0.4515 + 0.8049X_w + 0.0028X_v + 0.0102X_s$
(4)	L–P: 20–32 ppt	20	$Y = 0.1165 - 0.0098X_w + 0.0166X_v + 0.0335X_s$
(5)	L–P: 32–45 ppt	17	$Y = 0.1103 + 1.0291X_w - 0.0003X_v - 0.0021X_s$
(6)	S–P: 20–45 ppt	29	$Y = -0.6618 + 1.0004X_w + 0.0189X_v + 0.0030X_s$
(7)	S–P: 20–32 ppt	19	$Y = 0.1807 + 1.0003X_w + 0.0217X_v + 0.0021X_s$
(8)	S–P: 32–45 ppt	20	$Y = 0.1548 + 1.1085X_w + 0.0123X_v + 0.0064X_s$
(9)	L & S–U: 20–45 ppt	51	$Y = -0.0989 + 0.8243X_w + 0.0047X_v - 0.0009X_s$
(10)	L & S–P: 20–45 ppt	57	$Y = 0.3315 + 0.7857X_w + 0.0056X_v + 0.0066X_s$

* Not significant.
† L = large pinfish, S = small pinfish, U = unpolluted water, P = polluted water, L & S indicates large and small fish data have been combined, salinity range covered by regression is also indicated (e.g. 20–45 ppt).

Figure 1 is a summary of comparative metabolic trends calculated from regression equations for 50 and 150 gm fish in salinities of 20, 32 and 45 ppt with swimming velocities of 0 and 10 m/min. The 50 and 150 gm values are the approximate average weights of the pinfish used. The salinity values represent the averages of the salinities used. The zero swimming velocity represents an ecological "minimum" (Wohlschlag and Cameron, 1967). The 10 m/min. value is a velocity that both large and small fish can usually maintain for the duration of the experiment, although this velocity is probably near the maximum sustained activity level for small pinfish.

TABLE 4

Multiple regression statistics

Equation*	Degrees of freedom (N-1)	Standard error of estimate	F	P	Multiple correlation $R_{Y.WVS}$	P
(1) Large—U 20–45 ppt	26	0.1263	6.4426	P<0.005	0.6782	P<0.01
(2) Small—U 20–45 ppt	23	0.1127	0.2937	0.25<P	0.0648	0.5<P
(3) Large—P 20–45 ppt	26	0.1737	5.4762	P<0.005	0.6403	P<0.01
(4) Small—P 20–45 ppt	28	0.1558	14.8887	P<0.005	0.8000	P<0.01
(5) Large—P 20–32 ppt	19	0.1165	12.7741	P<0.005	0.8396	P<0.01
(6) Large—P 32–45 ppt	16	0.1103	11.3495	P<0.005	0.8498	P<0.01
(7) Small—P 20–32 ppt	18	0.1807	6.6565	0.05<P<0.025	0.8636	P<0.01
(8) Small—P 32–45 ppt	19	0.1548	15.6675	P<0.005	0.8636	P<0.01
(9) Large & Small—U Combined 20–45 ppt	50	0.1204	52.5801	P<0.005	0.8775	P<0.01
(10) Large & Small—P Combined 20–45 ppt	56	0.1688	52.8629	P<0.005	0.8675	P<0.01

* See Table 3 for explanation of this column.

The data in Figure 1 for small fish in unpolluted water were calculated from regression Equation 2 (Table 3), whose multiple correlation coefficient was not significant. However, this equation agreed very well with the regression equations by Wohlschlag and Cameron (1967) for pinfish at 20°C and 32 ppt.

After pinfish were subjected to hypersaline water for two weeks or to polluted water for several days, some would acquire a "ragged" appearance due to split fin membranes, bloody fins, and small areas devoid of scales with no indications that pathogens caused these changes. (Pinfish also tend to exhibit similar morbidity symptoms at sustained temperatures of 30°C or slightly higher).

DISCUSSION

UNPOLLUTED CONDITIONS

The influence of salinity on the respiration of both large and small pinfish was negligible in unpolluted water. The actual change in metabolic rates in the various salinities is 5% or less in all cases (Figure 1). Respiratory-salinity coefficients for both large and small pinfish are not statistically different from each other. Other studies have also shown that moderate salinity ranges have

	Standard errors of estimate for partial regression coefficients					
	Weight		Velocity		Salinity	
Equation*	b_w	P	b_v	P	b_s	P
(1) Large—U 20–45 ppt	0.2586	P<0.001	0.0053	0.4<P<0.5	0.0038	0.5<P
(2) Small—U 20–45 ppt	0.3179	0.5<P	0.0148	0.5<P	0.0029	0.5<P
(3) Large—P 20–45 ppt	0.2483	0.001<P<0.005	0.0067	0.5<P	0.0039	0.01<P<0.025
(4) Small—P 20–45 ppt	0.1838	P<0.001	0.0086	0.025<P<0.05	0.0030	0.2<P<0.4
(5) Large—P 20–32 ppt	0.2803	0.5<P	0.0057	0.001<P<0.005	0.0056	P<0.001
(6) Large—P 32–45 ppt	0.1847	P<0.001	0.0057	0.5<P	0.0039	0.5<P
(7) Small—P 20–32 ppt	0.2298	P<0.001	0.0147	0.1<P<0.2	0.0082	0.5<P
(8) Small—P 32–45 ppt	0.1956	P<0.001	0.0116	0.2<P<0.4	0.0068	0.2<P<0.4
(9) Large & Small—U Combined 20–45 ppt	0.0855	P<0.001	0.0041	0.2<P<0.4	0.0023	0.5<P
(10) Large & Small—P Combined 20–45 ppt	0.0750	P<0.001	0.0052	0.2<P<0.4	0.0024	0.005<P<0.01

* See Table 3 for explanation of this column.

only a small effect on the respiration of salt water fish (Kinne, 1964; Job, 1969; Moore and Wohlschlag, 1971). Both Gunter (1945) and Caldwell (1957) noted that pinfish appeared to be rather indifferent to salinity, although it is generally recognized that pinfish spawn in the more stenohaline coastal oceanic waters. Larger pinfish have been reported from nearly fresh water (Herald and Strickland, 1949) to hypersaline waters of 75 ppt (Simmons, 1957). The euryhaline nature of the larger pinfish implies that energy requirements for ionic and osmotic regulations are small.

Although salinity does not seem to affect the respiratory rate of pinfish, it does appear to affect the sustained swimming velocities, especially for large pinfish. In general, the maximum swimming velocities occurred in low salinity water while minimum swimming velocities occurred in hypersaline water. The average sustained swimming velocities of large pinfish decreases from 22.30 m/min. (131.2 body lengths/min.) at 20 ppt to 8.64 m/min (54.3 body lengths/min.) at 45 ppt. The average sustained swimming velocity of small pinfish decreased only from 10.93 m/min (107.4 body lengths/min.) at 20 ppt to 8.92 m/min. (75.0 body lengths/min.) at 45 ppt.

The decrease in sustained swimming velocity may be partly due to a hydrodynamical effect from increased water viscosity in higher salinities. There could be an increased hydrodynamical requirement for swimming due to density, although this seems doubtful since the change in density between 20 and 45 ppt

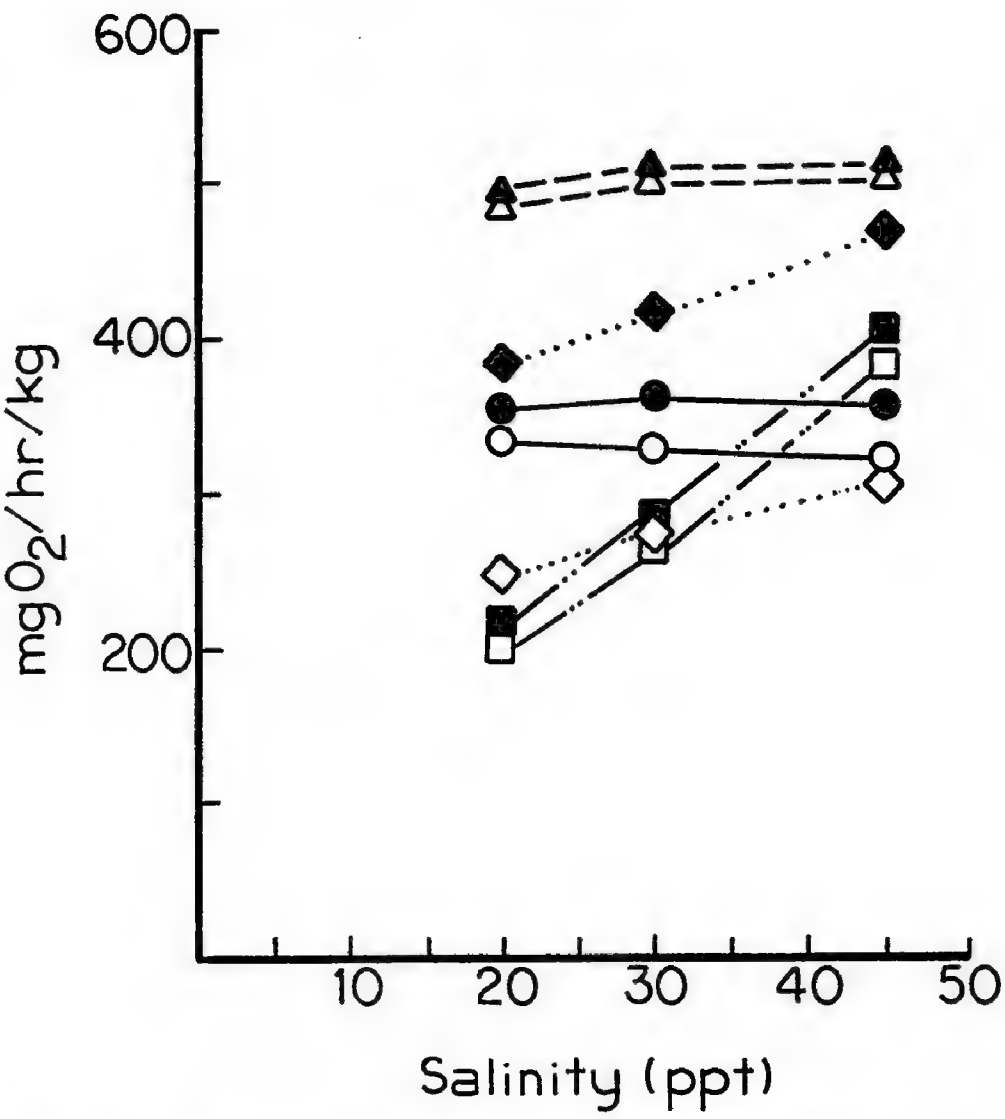

FIG. 1. The relationship of calculated metabolic rate (mgO_2/hr./kg) and salinity (ppt) for large (150 gm) and small (50 gm) pinfish in unpolluted and polluted water.

Open circles:	Large pinfish, unpolluted water, Om/min.
Closed circles:	Large pinfish, unpolluted water, 10m/min.
Open squares:	Large pinfish, polluted water, Om/min.
Closed squares:	Large pinfish, polluted water, 10m/min.
Open triangles:	Small pinfish, unpolluted water, Om/min.
Closed triangles:	Small pinfish, unpolluted water, 10m/min.
Open diamonds:	Small pinfish, polluted water, Om/min.
Closed diamonds:	Small pinfish, polluted water, 10m/min.

is very small. In two previous studies on salinity and activity in fish by Rao (1968) and by Farmer and Beamish (1969), neither attributed any change in energy requirements to changes in the mechanical surface drags in various salinities up to 30 ppt. For these reasons, it is anticipated that the *ad libitum* swimming velocity decreases would be due to biological effects of salinity stress.

The biological "condition" of the fish probably influenced their swimming velocities. Both large and small pinfish in salinities of 20 up to 32 ppt were visibly in better condition than those from hypersaline water (45 ppt). The reduction in sustained swimming velocity may also be the result of a shift in energy distribution among Kerr's (1971) major components of total metabolism, since the total metabolic rate of the pinfish changed only slightly in the various salinities. The amount of energy available for activity in the higher salinities might be

reduced with an accompanying compensatory decrease in sustained swimming velocity. Explanations of the physiological mechanisms to account for these observations are needed.

Both large and small pinfish apparently have little difficulty with metabolism in a salinity range of 20–45 ppt at 20°C in unpolluted water. Since only very slight metabolic changes were found over the salinity range, it would appear that salinity may not normally be an important variable for pinfish. However, only one temperature was used, 20°C, and since this temperature is apparently near the optimum level for swimming activity and tolerating sublethal pollution (Wohlschlag and Cameron, 1967), it may also be near the optimum temperature for salinity acclimation. Temperature can modify the effects of salinity, and maximum acclimation to salinity may be possible only at near-optimum temperatures (Kinne, 1964). Since 20°C occurs only briefly in the spring and fall, salinity may exert more of a stress at the higher or lower temperatures which pinfish normally encounter for longer periods of time under natural conditions. Wohlschlag and Cameron (1967) have shown that respiratory depression in pinfish due to sublethal pollution varies with temperature and is minimal at 20°C with greater depressions at 10 and 30°C. The upper lethal temperatures, along with food intake, food conversion and growth rates of fish can vary within the ranges of temperature and salinity found in the natural habitat (Kinne, 1960, 1964; Strawn and Dunn, 1967; Garside and Jordan, 1968).

POLLUTED CONDITIONS

The effluent chosen for this study is a common type of petrochemical pollution on the Gulf Coast. The data of Table 1 represents gross chemical characteristics only. The effects of this effiuent on fish in this study would be minimal since the experiments were conducted at high levels of oxygenation and moderate temperature, both of which would tend to eliminate labile volatile organic compounds and reactive chemical compounds such as sulfides. Hence, the pollution effects indicated in this study might be expected to be less than in the natural environment. Eisler (1965) found that salinity affected the toxicity of synthetic detergent concentrations in the mummichog, *Fundulus heteroclitus*. He theorized that some physiological stress was being placed on the mummichog osmoregulatory system which accounted for the differential toxicity at various salinities. It is believed that a similar situation might exist with the pinfish in which an interaction of the petrochemical effluent, salinity, and fish size would be reflected in the respiratory rate.

Wohlschlag and Cameron (1967) found that with a similar low level of pollution, the respiratory rates of both small (10 gm) and large (100 gm) pinfish were depressed (although differentially) at all temperatures tested. In another study which used the same effluent as in the present study, effluent concentrations up to 5% depressed the metabolic rate of pinfish, while concentrations from 5% to the TL_m of 8% caused metabolic loading (Steed and Copeland, 1967).

In the present study, the sublethal pollution depressed the metabolic rates of

small pinfish at all three salinities. Maximum metabolic depression was observed at 20 ppt and minimum depression occurred at 45 ppt. The zero swimming velocity metabolic rates were depressed over 40% in all salinities, but these depressed routine metabolic rates were still above the *standard* rate (about 100 $mgO_2/hr/kg$ at 30–35 ppt salinity) from Wohlschlag *et al* (1968). Pinfish tend to remain in a fairly irritable state under laboratory conditions, and because of this, metabolic rates would be expected to be higher than standard rates due to spontaneous activity at 0 m/min. The observed reduction in the 0 m/min metabolic rate may simply have been due to a reduction in spontaneous activity. The 10 m/min metabolic rates of small pinfish were not depressed nearly as much as the 0 m/min rates. This may be a reflection of less spontaneous activity being normally present in an actively swimming fish.

Sustained swimming velocities in polluted water showed the same general decrease as salinity increased as in unpolluted water, but the decreases were not as large (Table 2). Once again the sustained swimming velocities of large pinfish were decreased more than those of small fish. The sublethal pollution generally decreased the sustained swimming velocities of both large and small pinfish with salinities of 20 and 32 ppt. At 45 ppt, the pollutant did not seem to affect the sustained swimming velocities of either large or small pinfish.

With large pinfish, the effluent acted as a metabolic depressant at 20 and 32 ppt and apparently as a metabolic loading stress at 45 ppt (Figure 1). The b_w and b_s coefficients are statistically significant, but the small b_v coefficients are not significantly different from zero. Because the b_s coefficient is significant, there possibly was an interaction among the effluent, salinity and fish size factors involving the osmoregulatory system of the large pinfish. This interaction may involve increased energy requirements for the osmoregulatory system, which in turn may be associated with a decrease in the efficiency of the osmoregulatory system when the petrochemical effluent is present. Further multiple regression analysis showed the b_s and b_v coefficients, but not the b_w coefficient, to be statistically significant in the 20–32 ppt range. In the 32–45 ppt range, the b_w coefficient, but not the b_s or b_v coefficients, was significant. This would seem to indicate a further interaction among the effluent, salinity and weight factors that may affect the swimming efficiency of large pinfish.

At 45 ppt the effluent is possibly a loading stress for large fish instead of an inhibiting stress. In hypersaline water, the unusual relationship of large pinfish having higher zero velocity metabolic rates than small pinfish is found (Figure 1). Wohlschlag and Cech (1970) found that when using groups of large (83 gm) and small (33 gm) fish, the larger fish had higher zero velocity metabolic rates than small fish, at lower temperatures (10–20°C). They suggest that the higher rates of the large fish may be due to metabolic loading. Steed and Copeland (1967) also found metabolic loading in the pinfish with this effluent at normal salinities and a 25°C water temperature although at considerably higher concentrations (5–8%). In the present study, it appears likely that metabolic loading can occur for large fish in polluted water with a salinity at 45 ppt. Because, as indicated above, the sustained swimming velocities at 45 ppt with the pollutant were not substantially reduced, it may tentatively be assumed that the excess

metabolic requirements could be due to energy expended in spontaneous activity in addition to any energy excesses required for osmoregulatory work.

ECOLOGICAL IMPLICATIONS

The observed effects of salinity and sublethal pollution (depression and elevation of metabolic rates, poorer biological "condition" of fish, reduced sustained swimming velocities) would reduce the chances of survival of pinfish by affecting normal activities such as feeding and escaping predators. The end result would be an increase in mortality rate. A more subtle effect of the sublethal pollution and possibly salinity variations would be a reduction in growth rate and ultimate size of pinfish. As stresses increase maintenance costs, there is a subsequent decrease in energy available for growth. Kinne (1960, 1964) has shown that salinity can affect the growth rate and ultimate size of fish. Smith *et al.* (1966) found reduced growth rates with walleyes exposed to paper fiber wastes for long periods of time. Interestingly, they also found reduced active metabolic rates and an increase in split fin membranes, which are two conditions also observed in the present study. Lemke and Mont (1963) report reduced growth rates in bluegills exposed to sublethal concentrations of alkyl benzene sulfate. Gilderhus (1966) found reduced growth rates among blue gills exposed to sublethal concentrations of sodium arsenite with immature fish affected more than adults. Individuals within a population that have reduced growth rates either from pollution or salinity also would be subjected to natural mortality rates for the longer period required for reproductive maturity (Wohlschlag and Cameron, 1957). An increase in the mortality rates of small fish for any reason would thus decrease the number of fish surviving to the older, reproductive age classes. The mortality of mature, large fish would also be increased for the same reasons with a subsequent reducation of the exploitable and spawning stock.

The elevation of metabolism for large pinfish in polluted water with a salinity of 45 ppt, also could be detrimental to the population as a whole with the end results being increased mortality rates. In polluted hypersaline water, the large pinfish would require more oxygen than normal which would be a disadvantage since dissolved oxygen concentrations are usually lower in both hpyersaline and polluted water. Even if enough dissolved oxygen were available, it is doubtful that this presumed loading stress could be tolerated indefinitely. Black (1958) and many later workers have shown that hyperactivity can be lethal in fish due to a buildup in lactic acid which changes the acid-base balance in blood. With continuously elevated metabolic rates, a buildup of lactic acid could occur and eventually kill the fish, which again would reduce the spawning stock and the older age classes.

The overall result of environmental stresses such as sublethal petrochemical pollution and salinity variations would logically lead to a reduction in the size of individuals or a reduction in the size of a given pinfish population or both. This reduction would not be as sudden or as dramatic as the large fish kills that occur occasionally, but would occur over a period of years, assuming that spawning and recruitment could be maintained.

ACKNOWLEDGMENTS

We wish to thank Mr. Roy Spears of the Texas Parks and Wildlfie Department for the effluent analysis and Messrs. William Longley and Richard Watson for their assistance with the computer analysis.

This study was supported in part by National Science Foundation grant NSF-GB6889.

LITERATURE CITED

ALLEE, W. C., A. E. EMERSON, T. PARK, O. PARK, and K. P. SCHMIDT. 1949. *Principles of Animal Ecology*, xii + 837 pp. W. B. Saunders Co. Philadelphia.

BLACK, E. C. 1958. Hyperactivity as a lethal factor in fish. *J. Fish. Res. Bd. Canada* **15**(4): 573–586.

BRETT, J. R. 1958. Implications and assessments of environmental stress. *In The investigation of fish power problems.* H. R. MacMillan lectures in fisheries. P. A. Larken, editor, U. of British Columbia pp. 69–83.

————. 1971. Energetic responses of samlon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhyncus nerka*) *Am. Zool.* **11**: 99–113.

CALDWELL, D. K. 1957. The biology of the pinfish, *Lagodon rhomboides* (Linnaeus). *Bull. Fla St. Mus. biol. Sci.* **2**(6): 77–173.

CAMERON, J. N. 1969. Growth, respiratory metabolism, and seasonal distribution of juvenile pinfish (*Lagodon rhomboides* Linneaus) in Redfish Bay, Texas. *Contr. mar. Sci. Uni. Texas.* **14**: 19–36.

CARRITT, D. E. and J. H. CARPENTER. 1967. Comparison and evaluation of currently employed modifications of the Winkler method for determining dissolved oxygen in sea water; a NASCO report. *J. mar. Res.* **24**(3): 286–318.

COPELAND, B. J. and D. E. WOHLSCHLAG. 1968. Biological responses to nutrients—eutrophication: saline water considerations. *In Advances in Water Quality Improvement.* Gloyna, E. F. and W. W. Eckenfelder, Jr. (eds.). 513 pp. U. T. Press.

EISLER, R. 1965. Some effects of a synthetic detergent on estuarine fishes. *Trans. Am. Fish. Soc.* **94**(1): 26–31.

FARMER, G. J. and F. W. H. BEAMISH. 1969. Oxygen consumption of *Tilapia nilotica* in relation to swimming speed and salinity. *J. Fish. Res. Bd Canada* **26**: 2807–2821.

GARSIDE, E. T. and E. M. JORDAN. 1968. Upper lethal temperatures at various levels of salinity in the euryhaline cyprinodontids *Fundulus heteroclitus* and *F. diaphanus* after isosmotic acclimation. *J. Fish. Res. Bd Canada* **25**(12): 2717–2720.

GILDERHUS, P. A. 1966. Some effcets of sublethal concentrations of sodium arsenite on bluegills and the aquatic environment. *Trans. Am. Fish. Soc.* **95**(3): 289–296.

GUNTER, G. 1945. Studies on the marine fishes of Texas. *Publs Inst. mar. Sci. Univ. Tex.* **1**(1): 1–190.

————. 1961. Some relationships of estuarine organisms to salinity. *Limnol. Oceanogr.* **6**(2): 182–190.

HERALD, E. S. and R. R. STRICKLAND. 1949. An annotated list of the fishes of Homosassa Springs, Florida. *Q. Jl. Fla Acad. Sci.* **11**(4): 99–109.

HICKMAN, C. P. JR. 1959. The osmoregulatory role of the thyroid gland in the starry flounder *Platichthys stellatus. Can. J. Zool.* **37**: 997–1060.

JOB, S. V. 1959. The metabolism of *Plotosus anguillaris* (Bloch) in various concentrations of salt and oxygen in the medium. *Proc. Indian Aacd. Sci.* B **50**: 267–288.

————————. 1969. The respiratory metabolism of *Tilapia mossambica* (Teleostei). I. The effect of size, temperature, and salinity. *Mar. Biol.* **2:** 121–126.

KERR, S. R. 1971. Analysis of laboratory experiments on growth efficiency of fishes. *J. Fish. Res. Bd Canada* **28:** 801–808.

KEYS, A. B. 1931. A study of the selective action of decreased salinity and of asphyxiation on the Pacific killifish, *Fundulus parvipinnis*. *Bull. Scripps Instn Oceanogr. tech. Ser.* **2**(2): 417–490.

KINNE, O. 1960. Growth, food intake, and food conversion in a euryplastic fish exposed to different temperatures and salinities. *Physiol. Zool.* **33:** 288–317.

————————. 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinaitons. *Oceanogr. Mar. Biol. Ann. Rev.* **2:** 281–339.

LEMKE, A. E. and D. I. MOUNT. 1963. Some effects of alkyl benzene sulfonate on the bluegill. *Trans. Am. Fish. Soc.* **92**(4): 372–378.

MOORE, R. H. and D. E. WOHLSCHLAG. 1971. Seasonal variations in the metabolism of the Atlantic midshipman, *Porichthys porosissimus* (Valenciennes). *J. exp. mar. Ecol.* **7:** 163–172.

PARRY, G. 1966. Osmotic adaptation in fishes. *Biol. Rev.* **41:** 392–444.

PARVATHESWARARAO, V. 1965. Influence of different temperature-salinity combinations on the oxygen consumption in the fresh water fish *Etroplus maculatus* (Teleostei). *Helgolander wiss. Meeresunters.* **12**(3): 302–314.

RAO, G. M. M. 1968. Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. *Can. J. Zool.* **46:** 781–786.

SIMMONS, E. G. 1957. An ecological survey of the upper Laguna Madre of Texas. *Publs Inst. mar. Sci. Unv. Tex.* **4**(2): 156–200.

SMITH, L. L., JR., R. H. KRAMER, and D. M. OSEID. 1966. Long-term effects of conifer-ground-wood paper fiber on walleyes. *Trans. Am. Fish. Soc.* **95**(1): 60–70.

STEED, D. L. and B. J. COPELAND. 1967. Metabolic responses of some estuarine organisms to an industrial effluent. *Contr. mar. Sci. Univ. Tex.* **12:** 143–159.

STRAWN, K. and J. E. DUNN. 1967. Resistance of Texas salt- and fresh-water marsh fishes to heat deaths at various salinities. *Tex. J. Sci.* **19**(1): 57–76.

SUBRAMANIAN, A. 1967. Oxygen consumption in the worm eel *Moringua linearis* (Gray) in relation to size and salinity. *Proc. Indian Acad. Sci. Sec.* B **66**(6): 273–278.

UMMINGER, B. L. 1971. Patterns in freshwater fishes at temperatures near freezing. *Physiol. Zool.* **44:** 20–27.

WOHLSCHLAG, D. E. 1957. Differences in metabolic rates of migratory and resident freshwater forms of an Arctic whitefish. *Ecology* **38:** 502–510.

————————, and J. N. CAMERON. 1967. Assessment of a low level stress on the respiratory metabolism of the pinfish (*Lagodon rhomboides*). *Publs Inst. mar. Sci. Univ. Tex.* **12:** 160–171.

————————, J. N. CAMERON and J. J. CECH. 1968. Seasonal changes in the respiratory metabolism of the pinfish (*Lagodon rhomboides*). *Contr. mar. Sci. Univ. Tex.* **13:** 89–104.

———————— and J. J. CECH, JR. 1970. Size of pinfish in relation to thermal stress. *Contr. mar. Sci. Univ. Tex.* **15:** 21–31.

STABLE CARBON ISOTOPE RATIO VARIATIONS IN THE ORGANIC CARBON FROM GULF OF MEXICO SEDIMENTS

P. L. Parker, E. Wm. Behrens, John A. Calder* and David Shultz*

Marine Science Institute, University of Texas at Austin

ABSTRACT

The organic carbon was extracted from 106 samples of six piston cores of abyssal sediments in the eastern Gulf of Mexico by combustion in a radio frequency furnace and collection of the CO_2 by freezing in a vacuum line. The CO_2 was transferred to a mass spectrometer and the ratio of stable carbon isotopes was measured. Major δC^{13} variations correlate with the changes from yellowish, foraminiferal ooze at the tops of cores to olive grey clays deeper in the cores. The lithologic changes are correlated with the Holocene-Pleistocene transition from marine pelagic sedimentation to glacial stage turbidity current deposition. The isotopically heavier carbon in the oozes is typical of pelagic marine values while the carbon in the clays is lighter and probably of terrestrial origin. Some of the cores near the continental margins apparently penetrate through the last interglacial stage which is characterized by a transition similar to that at the Pleistocene-Holocene boundary.

INTRODUCTION

In a detailed survey of variations of stable carbon isotope ratios of the major carbon reservoirs, Craig (1953) noted that δC^{13} values of total organic carbon from Holocene nearshore sediments ranged between −10.8 and −22.6 per mil. Landergren (1954) reported that several samples from deep sea cores from the Atlantic and Pacific Oceans ranged between −24.6 and −19.5, but he recognized no trends with depth or location. Eckelman, Broecker, Whitlock and Allsup (1962) noted that the δC^{13} values for the deeper samples from a core from the Cariaco Trench and one from the Mediterranean Sea were 2 to 3 per mill more negative than upper samples. In the case of the Mediterranean core they suggested that more C^{13} depleted land derived organic matter might cause the shift.

Sackett and Thompson (1963) brought the problem of δC^{13} shifts caused by land derived organic matter, into clear focus in the case of nearshore marine sediments. Sackett (1964) extended this concept into the deep ocean by comparing 3 cores from the Gulf of Mexico abyssal plain to 3 cores from the Sigsbee

* Present address: Dept. of Oceanography, Florida State Univ., Tallahassee, Florida 32306

TABLE 1

Location of core stations from KANE Cruise (June–September, 1969)

Station number position depth (fms)	Core length (cm)	Physigraphic province
28 23° 40′ N 84° 40′ W 1845	940	sill, Yucatan straits
68 28° 15′ N 88° 22′ W 1883	920	Mississippi Cone
83 24° 29.7′ N 89° 30.9′ W 3572	920	Edge of Sigbee Deep
47 26° 35′ N 86° 25′ W ?	978	East basin
52 27° 13′ N 85° 26.8′ W 1730	841	Edge of Florida scarp
60 26° 34.8′ N 89° 18′ W 2863	176	Mississippi Cone

Knolls. The Knolls cores were fairly uniform in δC^{13} indicating a marine source of the organic matter. In one of the abyssal plain cores there was a clear shift in δC^{13} toward more negative values at approximately 94 cm. Sackett states that these shifts are "associated with the Wisconsin ice age, when, due to lowering of sea level, the detrital load of the Mississippi River was deposited in the Gulf of Mexico beyond the present day continental shelf."

We here report on similar studies on piston cores taken during the 1969 cruises of the ELISHA KANE in the Gulf of Mexico.

MATERIALS AND METHODS

The samples for organic analyses were taken soon after the cores were raised, usually within a few hours. The locations are given in Table 1. They were frozen at the time of collection and stored frozen. Thawed samples were treated with dilute hydrochloric acid to remove carbonate, filtered, washed and dried at 40°C. Weighed portions of dried and powdered samples were combusted in a Leco radio-frequency furnace and the evolved CO_2 collected in an attached vacuum line. The volume of CO_2 was measured manometrically, and set aside in sample bulbs for mass spectrometry.

The Leco combustion system has not been described in our earlier publications. Since it was developed as a rapid method to prepare samples for mass spectrometric analysis other workers may be interested in the details of its operation. The method is based on mating a simple vacuum line to a standard Leco (Laboratory Equipment Company) radio-frequency furnace (Fig. 1).

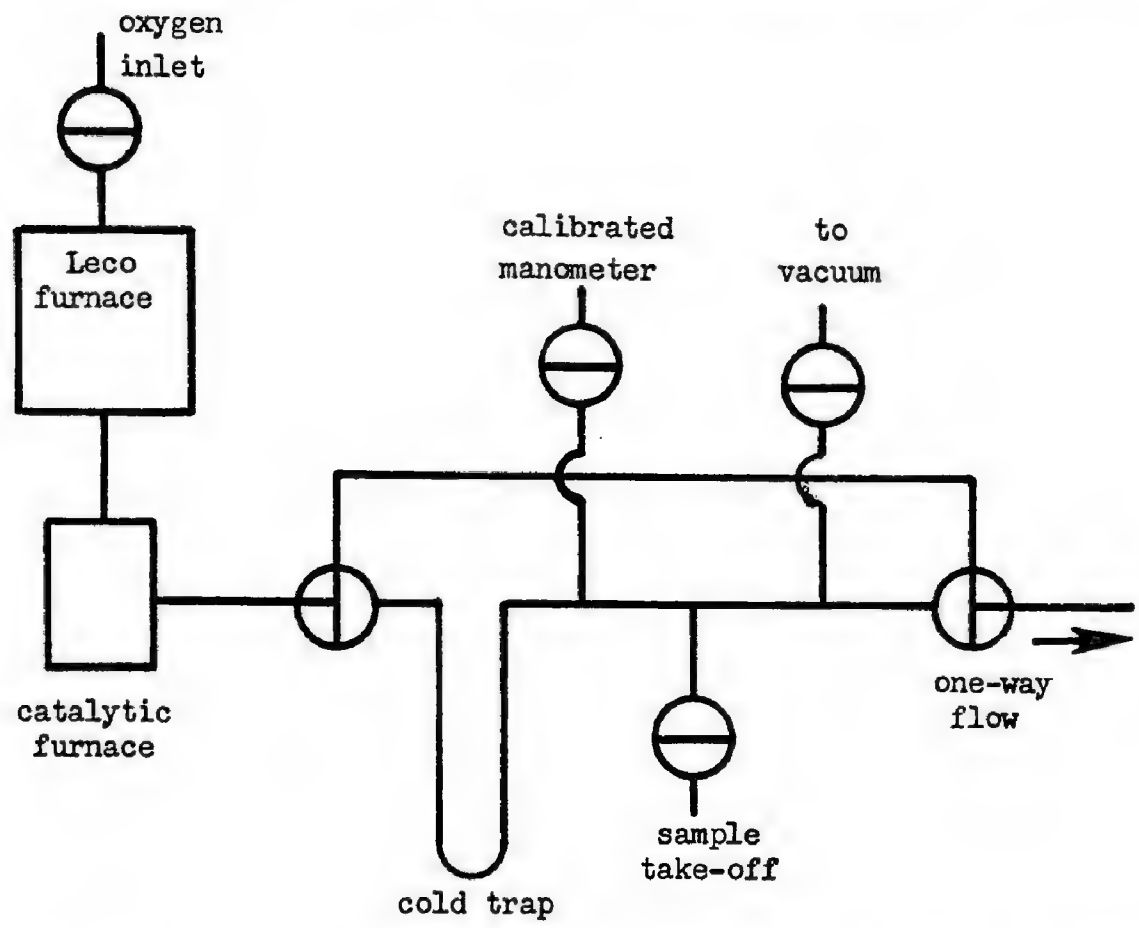

FIG. 1. Schematic diagram of the combustion–vacuum line used to convert the organic carbon in a sediment sample to CO_2 for mass spectrometry. See text for discussion.

The weighed sample was placed in a Leco clay crucilbe along with 5 g each of wire-form copper oxide and iron pellets. The exact order of addition of these materials varies somewhat with operator but it is important to have the CuO well mixed with the sample. After the lid was put on the crucible it was placed in the coils of the Leco furnace. The system was flushed with high purity oxygen for 30 seconds (30 ml/min) and vented through the one way flow which was in fact a second mercury manometer. Then the two three-way stopcocks were turned so that the O_2 flowed to the cold trap which was at this point cooled with liquid nitrogen. The 2 one-minute burns were carried out allowing the crucible to get red hot during the second one. The products of combustion were swept by the O_2 through the catalytic furnace and into the cold trap. Under these conditions CO_2, H_2O and O_2 are condensed. Since the vapor pressure of oxygen is 17 cm at liquid nitrogen temperature the system is a closed flow system. The catalytic furnace was a tube furnace (550°C) packed with CuO and MnO_2 which served to remove any oxides of nitrogen and sulfur. After the combustion and a one minute flushing time the three way stopcocks were closed to isolate the U-tube cold trap and the stopcock to the vacuum pump cracked. In this way the O_2 was slowly pumped away after which the stopcock to vacuum was closed. Next the liquid nitrogen was replaced by a dry-ice-alcohol bath to retain water vapor and the CO_2 was frozen into the pre-evacuated sample take-off bulb. In cases where the % carbon was needed the volume of CO_2 was measured on the calibrated manometer. A complete combustion can be carried out in less than 10 minutes.

The use of this system requires care in using the same times for combustion and pumping so that a new operator will usually require several days to obtain satisfactory results. There is a potential hazard to the vacuum line as it was first designed. That is, should the liquid nitrogen be removed before the O^2 was pumped away the pressure would rise quickly. This can be avoided by never closing the stopcock to the calibrated manometer, or better by not installing a stopcock at this point. In later models we found it desirable to insert a glass-wool or glass-frit on the vacuum side of the U-tube cold trap to prevent the liquified O_2 from splashing during pump-off.

Samples, prepared by the Leco method were within ± 0.2 per mil of the value obtained using the standard Craig (1953) method. Samples can be reprducibly combusted by the Leco

TABLE 2

Analytical data for six Gulf of Mexico cores

#28			#68			#83		
Interval	del-C^{13}	Percent C*	Interval	del-C^{13}	Percent C	Interval	del-C^{13}	Percent C
10	—19.6	0.7	0	—18.7	0.95	10	—19.3	0.5
20	—19.5	0.5	10	—18.8	.85	20	—19.6	0.6
40	—20.1	0.5	20	—18.9	.85	40	—19.7	0.6
60	—22.4	0.4	40	—19.0	.85	60	—19.2	1.7
80	—23.8	0.9	60	—19.2	.95	80	—23.4	0.4
140	—23.8	1.0	80	—23.3	1.60	100	—20.3	0.6
200	—23.6	1.0	100	—24.2	1.15	150	—24.1	1.2
260	—23.6	0.9	150	—23.7	1.10	200	—24.7	1.3
320	—23.7	1.1	200	—23.8	1.15	250	—24.5	1.1
380	—23.7	1.0	250	—23.5	1.50	300	—24.7	1.0
440	—23.6	1.0	300	—23.8	1.60	350	—24.4	1.2
520	—23.2	1.1	350	—22.0	1.00	400	—24.7	1.0
540	—20.7	0.7	400	—25.1	.95	450	—24.6	1.3
560	—22.9	0.7	450	—24.3	.95	500	—24.6	1.1
580	—21.1	0.8	500	—24.6	.97	550	—23.9	1.1
600	—24.0	0.9	550	—24.5	1.45	600	—24.8	1.0
660	—24.5	1.4	600	—24.8	.98	650	—24.5	1.2
720	—24.4	1.4	650	—24.9	1.15	700	—24.0	1.3
780	—24.3	1.1	700	—23.8	.98	750	—24.1	1.2
840	—24.5	1.2	750	—24.5	1.15	800	—25.0	1.4
900	—24.3	1.2	800	—25.2	1.12	850	—23.9	1.3
			850	—24.6	1.16	900	—24.1	0.9
			900	—24.6	1.13			

#47			#52			#60		
Interval	del-C^{13}	Percent C*	Interval	del-C^{13}	Percent C	Interval	del-C^{13}	Percent C
10	—22.6	0.5	10	—24.0	2.8	5	—21.6	0.70
25	—23.9	0.2	40	—24.4	2.0	15	—20.9	0.45
40	—23.8	0.5	60	—24.4	1.4	21	—18.8	0.50
60	—24.7	0.8	80	—24.5	1.1	30	—21.4	0.25
80	—24.6	1.2	100	—24.3	1.2	40	—20.9	0.70
100	—24.4	1.3	260	—25.1	0.8	60	—21.6	0.55
160	—24.6	1.2	320	—24.5	0.7	80	—22.3	.75
220	—24.9	1.0	380	—24.4	1.1	100	—22.4	.95
300	—24.7	1.5	440	—24.2	0.9	120	—22.1	.85
400	—24.8	1.5	503	—24.5	1.1	140	—21.9	.75
500	—25.1	1.2	600	—24.6	0.9	171	—21.2	1.25
710	—24.8	1.3	680	—23.8	0.3			
710	—24.8	1.3	680	—23.8	0.3			
800	—24.4	1.3	740	—24.3	1.2			
875	—24.4	0.8	800	—24.4	1.2			
967	—24.4	1.0						

* The del-C^{13} and Percent C are based on the organic carbon in the acid insoluble residue.
The intervals are in cm.

method to within ± 0.1 per mil, although 0.2 is a more realistic value if one wishes to take advantage of the speed of the method. Finally it should be obvious that highly volatile samples may not be prepared by the Leco method although we were able to run several petroleum samples.

Isotope ratio measurements were performed with a six inch, 60° sector mass spectometer. The instrument (Model 6-60-RMS) was built by Nuclide Corporation, State College, Pa. The experimental quantity obtained from the mass spectrometer is δC^{13}.

$$\delta C^{13}\,‰ = \frac{(C^{13}/C^{12})\text{ sample} - (C^{13}/C^{12})\text{ std}}{(C^{13}/C^{12})\text{ std}} \times 1000$$

Our measurements are reported with respect to a National Bureau of Standards Isotope Reference Material, NBS-20. The standard, PDB, used by many workers is + 1.06 on this scale. Where our data is directly compared to that of others account will be taken of the different standards. The working standard was corrected for oxygen errors according to the method of Craig (1957). In most cases, where the sample and standard were prepared using the same tank oxygen and CuO packed furnace, and where the sample and standard have similar δC^{13} values the individual δO^{18} values were not measured and the correction factor not applied to individual samples.

RESULTS AND DISCUSSION

The distribution of δC^{13} values and the percent total organic carbon (TOC) with depth in each core is shown in Table 2 and Figure 2. The values all fall within the range for other non-calcareous marine sediments. The most striking feature of the data is the sharp shif in δC^{13} within the top meter of cores 28, 47, 68 and 83 (Fig. 2). This shift is usually associated with a change from light colored foraminiferal ooze at the tops of the cores to olive gray colored clayey mud below. Similar transitions in sediment types in deep sea cores have been shown to correlate with the Holocene-Pleistocene boundary (e.g., Ewing et al., 1958), and we assume the same correlation here.

Two explanations have been offered for the decrease in δC^{13} across the Holocene-Pleistocene boundary. Rogers and Koons (1969) suggested that planktonic organisms produced isotopically lighter organic carbon when surface water temperature was lower. Both kinetic and equilibrium isotope effects are temperature dependent. A lower temperature of the environment would tend to increase fractionation factors so that organic matter would be more negative whether it was marine or terrestrial. However, Sackett and Rankin (1970) have recently concluded that the temperature required to obtain the observed δC^{13} values on a straight chemical basis is too low relative to the sea surface temperatures estimated by the oxygen isotope paleotemperature method.

A more probable explanation is Sackett's (1964) suggestion that the lighter carbon in Pleistocene sediments is ultimately derived from land plants. These organisms contributed more organic matter to deep sea sediments during glacial stages when sea level was much lower, and rivers carried their eroded detritus to the continental shelf edge from where it was periodically transferred to the abyssal basins by turbidity currents. Since the terrestrial input model and the temperature dependence of isotope effects model act in the same direction, one

must conclude that both phenomena are active but that the terrestrial input model seems to be dominant.

The pre-Holocene lower parts of the cores studied contain less striking but significant variations in δC^{13}. The part of the Gulf of Mexico from which these cores were obtained is entirely within the Mississippi Cone as defined by Ewing et al. (1958). The source of the sediment making up this cone is the Mississippi River. Radiocarbon dates (Ewing et al., 1958) indicate that the transition from Holocene to Pleistocene, usually within two meters of the top of the cores taken in this area, was generally accompanied by an increase in the rate of sedimentation from the Mississippi Source sometimes as great as 20 fold. Thus during the last glacial stage there was a sufficient thickness of sediment deposited so that most of our cores did not penetrate to a horizon representing the next, warm, interstadial or interglacial stage.

Core 28 is an exception to this generalization. From 524 to 611 cm depth the olive gray clayey mud is interrupted by a burrowed, yellowish, foraminiferal ooze or marl. This material appears very similar to the surface sediment and its organic carbon has nearly the same δC^{13}. It is reasonable to expect less sediment to have been deposited at the locality of this core than over the rest of the abyssal plain, because it is most distant from the sediment source, the mouth of the Mississippi River. Below 600 cm the sediment becomes an olive gray clay again, and δC^{13} decreases just as it does below the surface ooze. The decrease is to a lower average value (−24.4), however, than the value for the upper clay (−23.7). Although this difference is small, its significance can be seen from the fact that the data for the two sections have no overlap (Table 2).

In core 68 there is no major litholoigc break below the Holocene-Pleistocene transition, but at 350 cm a high δC^{13} value suggests a brief interglacial or interstadial period. Correlation with the 524 to 611 cm interval in core 28 would be very weak on the basis of a single sample, but it is strengthened a great deal by the almost identical difference between the δC^{13} values for the olive gray clays above and below this interval (−23.7 and −24.6 respectively). A lower rate of sedimentation allowing penetration to an older horizon at the locality of this core is also plausible. This locality is 1,000 meters higher on the Mississippi Cone than the other cores. Such a site may be bypassed by much of the sediment being carried from the river mouth to the deeped abyssal plain.

If cores 28 and 68 penetrated to older horizons than the other cores, then the δC^{13} values for the other cores should correlate with the upper parts of cores 28 and 68, i.e., with an average δC^{13} of about −23.7. Table 2 shows that this is not the case. The average δC^{13} values for cores 52, 47, and 83 are much closer to the average values for the lower rather than for the upper parts of cores 28 and 68. Anomalous values for core 60 may have resulted from disturbance by the coring operating during which the core barrel was bent and less than 2 meters of core was recovered.

The absence of the expected correlation might be explained in either of two ways. First, the upper parts of cores 28 and 68 may represent deposition that was restricted to a marginal portion of the Gulf basin during the latest part of the Wisconsin Stage, perhaps during post-Farmdalian time. In this case the deeper,

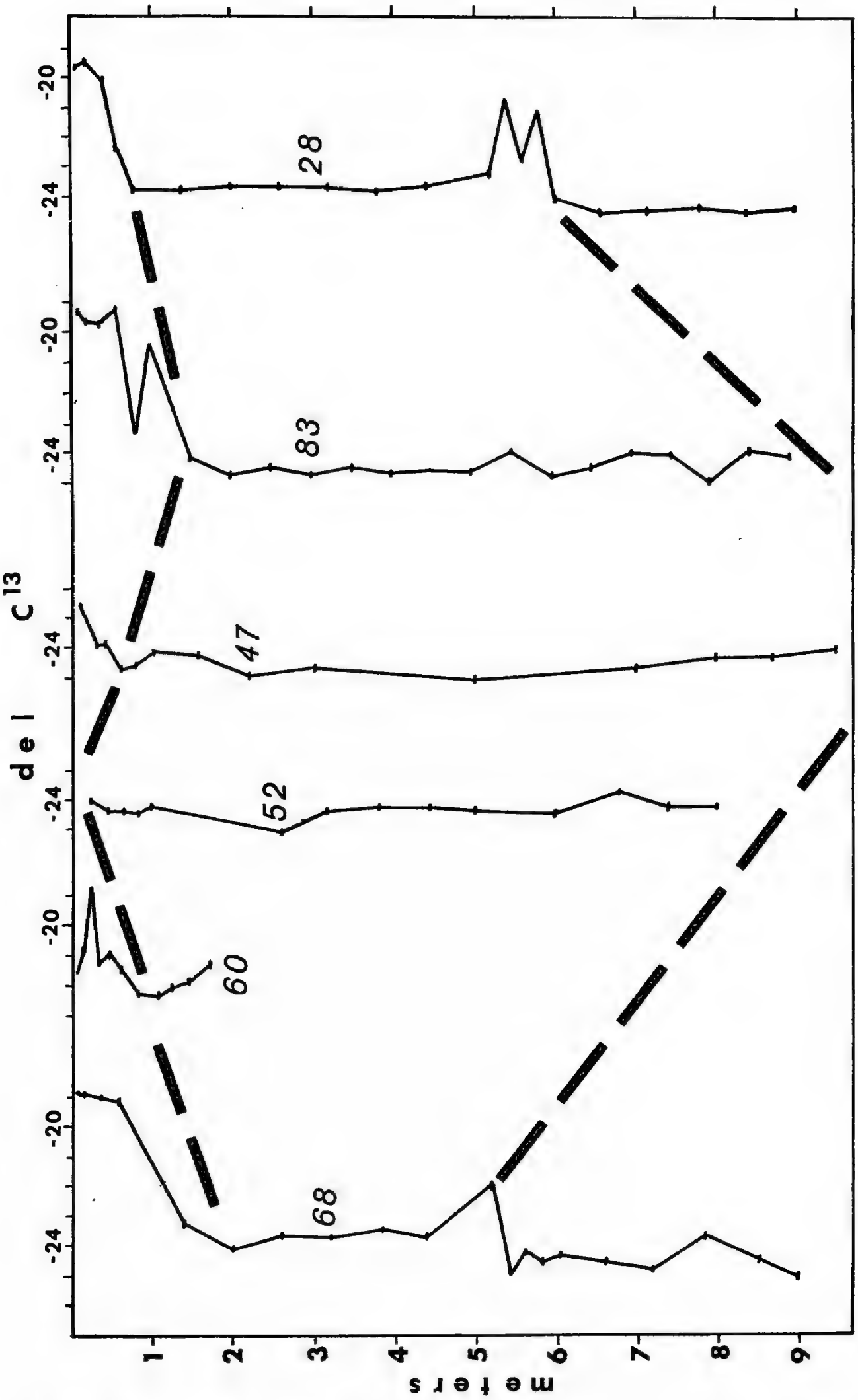

FIG. 2. Core logs showing del C^{13} vs. depth. Cores are arranged from left to right in order of increasing distance from the mouth of the Mississippi River. Upper dashed line is suggested as the Holocene&Pleistocene boundary; lower dashed line probably correlates an interstadial period within the Wisconsin. See text for discussion.

isotopically heavy horizons in cores 28 and 68 should have ages of about 25,000 to 30,000 years B.P. However, there is insufficient material available for radiocarbon dating of this interval; so further speculation concerning this hypothesis should be postponed until more data can be obtained.

Secondly, the stratigraphy may be correct, but the organic carbon deposited at the sites of cores 28 and 68 may have been isotopically different from the material deposited simultaneously at the other sites. There is no evidence suggesting separate sources for the terrestrial material; but the mixture of terrestrial and marine carbon may be richer in the latter than the mixtures in the cores from other sites. The enrichment in marine carbon may be due to greater productivity resulting, in turn, from nutrient enrichment near the mouth of the Mississippi River and from upwelling associated with water movement south along the Florida shelf. However, uniform productivity of marine carbon could also occur, because a lower rate of turbidite sedimentation would result in less dilution of the marine carbon by terrestrial carbon at the sites of the cores apparently penetrating to older horizons.

Breaks in δC^{13} vs depth curves were observed by Rogers and Koons (1969) in 1000-ft drill cores from the slope of the Gulf of Mexico. While they did not observe the fine structured break in the upper 30-ft, they found several similar breaks in the 1000-ft column.

Oceanic Holocene organic carbon at many locations has a δC^{13} of -18 to -20. Values reported which are more negative, -22 to -26 appear to be due to missing the uppermost part of the core. The -18 to -20 range has been found in the Gulf of Mexico, the Mediterranean, the Caribbean, the S. Atlantic and the Equatorial Atlantic. In addition Degens (1969) quotes unpublished data of J. A. Hunt and K. O. Emery for the Indian Ocean, the Southwest Pacific and the North Atlantic which fall into the stated range. Departures from this range, such as reported here, require massive shifts in the carbon cycle. It is concluded that the Pleistocene shifts result from a long and intensive input of land derived organic matter into oceanic basin.

LITERATURE CITED

CRAIG, H. 1953. The geochemistry of the stable carbon isotopes. *Geochemc. cosmochim. Acta.* **3:** 53–92.

————. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochim. Cosmochim. Acta.* **12:** 133–149.

DEGENS, E. E. 1969. The biochemistry of stable carbon isotopes, p. 304–328. *In: Organic Geochemistry*, G. Eglinton and M. T. J. Murphy (ed.). Springer-Verlag, New York.

ECKELMAN, W. R., W. S. BROECKER, D. W. WHITLOCK and J. R. ALLSUP. 1962. Implications of carbon isotopic composition of total organic carbon of some recent sediments and ancient oils. *Bull. Am. Ass. Petrol. Geol.* **46:** 699–704.

EWING, M., D. B. ERICSON and B. C. HEEZEN. 1958. Sediments and topography of the Gulf of Mexico, p. 995–1054. *In: Habit of Oil*, Lewis G. Weeks (ed.). Am. Assoc. Pet. Geol., Tulsa, Okla.

LANDERGREN, S. 1954 On the relative abundance of the stable carbon isotopes in marine sediments. *Deep Sea Res.* **1:** 98–120.

ROGERS, M. A. and C. B. KOONS. 1969. Organic carbon C^{13} values from Quarternary marine sequences in the Gulf of Mexico: a reflection of paleotemperature changes. *Trans. Gulf-Cst. Assoc. Geol. Socs.* **19**: 529-534.

SACKETT, W. M. and R. R. THOMPSON. 1963. Isotopic organic carbon composition of recent continental derived clastic sediments of eastern Gulf coast, Gulf of Mexico. *Bull. Am. Ass. Petrol. Geol.* **47**: 525–531.

SACKETT, W. M. 1964. The depositional history and isotopic organic carbon composition of marine sediments. *Marine Geology*. **2**: 173–185.

SACKETT, W. M. and J. G. RANKIN. 1970. Paleotemperatures for the Gulf Coast of Mexico. *J. geophys. Res.* **75**: 4557–4560.

This research was supported by funds made available to us by the Graduate Dean (NSF GZ 074) and by NSF grant GA-911. The samples were collected as part of a joint effort by the U.S. Geological Survey, Marine Geology Branch, the U.S. Navy Oceanographic Office and several universities. We are grateful to the Navy for the use of KANE, to the crew of the KANE and to Henry Berryhill of the USCG who did all the paperwork which made our work easy.

LIPID GEOCHEMISTRY OF A MISSISSIPPI COASTAL BOG ENVIRONMENT

Julia R. Sever

Louisiana State University
Baton, Rouge, Louisiana 70803

Thomas F. Lytle

Gulf Coast Research Laboratory
Ocean Springs, Mississippi 39564

Pat Haug

Geochemisches Institut
der Universitat Gottingen, Germany

ABSTRACT

The lipid composition of a group of primitive higher plants from a Mississippi bog environment have been investigated from an organic geochemical point of view. The plants studied include mosses, clubmosses, ferns and flowerplants. The hydrocarbon and fatty acid patterns were obtained and other group lipid separations made. While most of the patterns found were similar to other plants, a C-28 n-alkane was found in high concentration in the clubmoss, *Lycopodium*. The plant alkane and fatty acid patterns were correlated with sediment lipids.

INTRODUCTION

Organic-rich coastal bogs span the Mississippi Gulf Coast. The primary producers in the bogs are a large array of plants. The lush growth furnishes large amounts of decaying plant debris producing rich organic sinks. These bogs are important for several reasons among them being their aesthetic value. A unique group of plants inhabits the bogs including several species of native orchids. The bogs are also of potential economic importance as a fuel source since under proper conditions bogs have served as sources of geologically old coal deposits. Therefore similar environments of the past can be considered "fingerprints" of these coastal bogs of today. However, these bogs have never been studied from a chemical standpoint. Intrusion by industrial expansion has already destroyed many of these extraordinary environments by draining and/or filling them; future plans indicate eradication of the remaining bogs in Mississippi. One of these very unusual areas was chosen for study. Dominant plant types were identified and col-

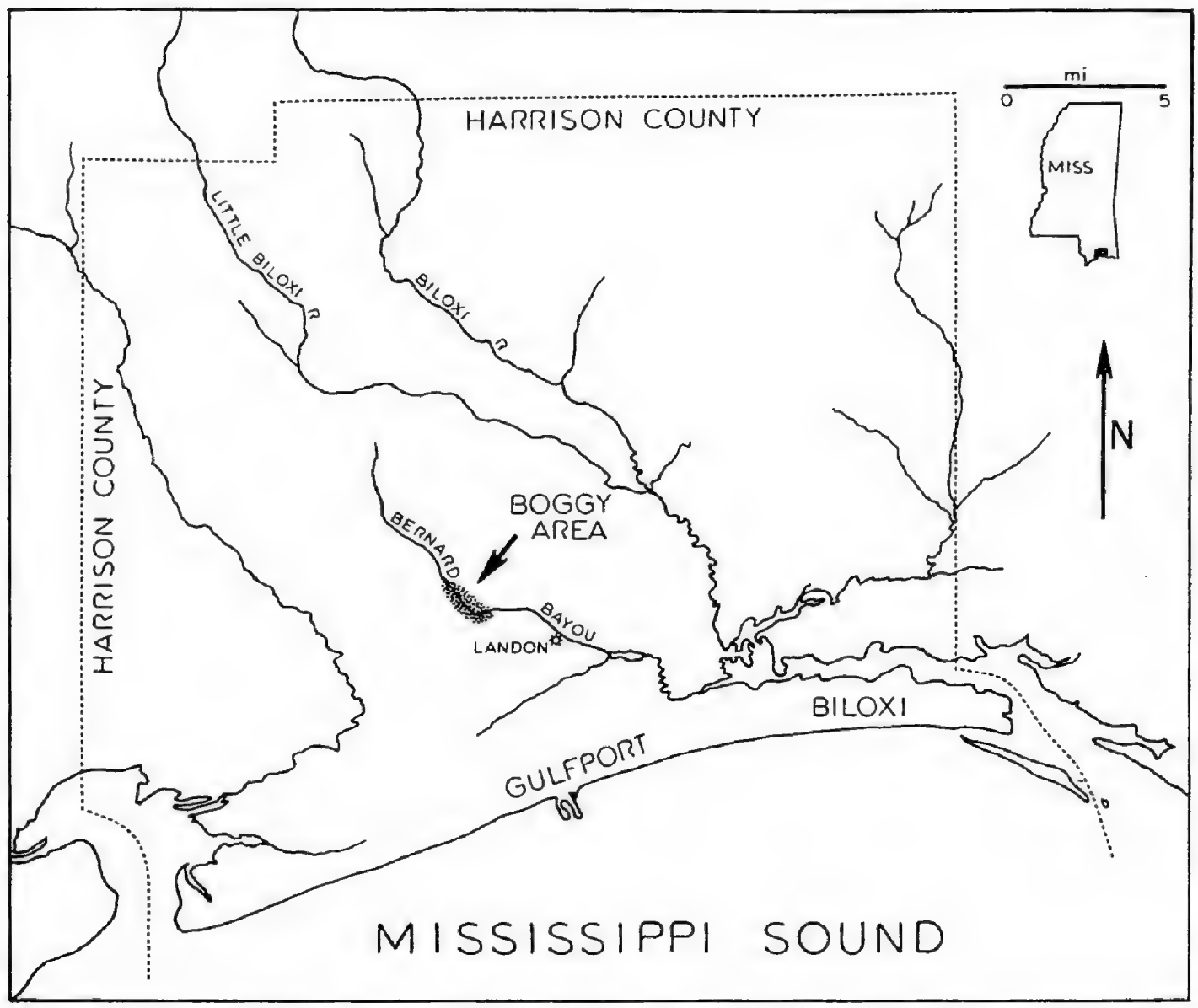

FIG. 1. Map of Study area.

lected during the flowering stage of growth for chemical analyses. At the same time, top sediment samples were also collected for chemical analyses.

The bog was located in a region paralleling Bernard Bayou about six miles from the Gulf coast, as indicated in Figure 1. The exact extent of the bog has not been determined, but it does extend for at least a quarter mile along the bayou. The soil profile is characterized by at least thre distinct layers. The top two peaty layers, varying in depth from 2 to 6 feet, grade from the top layer, consisting of an acid, Portsmouth, sandy loam of high organic content containing many plant fragments, to a layer of more homologenous plant remains and higher sand content. These two layers are underlain by an almost impervious layer of sand. This "sand pan" probably accounts for the tenacity of this bog for water (Eleuterius, 1968; Eleuterius and Jones, 1969).

The plant composition of bogs varies considerably with location. This particular bog is situated on the edge of the Pliocene-Miocene escarpment, which runs in a generally east-west direction across Mississippi, and differs in plant distribution from those bogs located north and south of the escarpment. Plant composition of bogs is also vastly affected by fire, which helps maintain lower plant dominance. Plants were collected in a season following a burn-out so that woody-sedge plants were reduced to a minimum.

Three of the four divisions of the plant kingdom were represented at the major plants contributing to the bog under invstigation: *Bryophyta* (Mosses and Liverworts), *Pteridophyta* (ferns), and *Spermatophyta* (seed plants). (See Table 1 for classification of plants collected.) It is of interest that these bogs support large amounts of lower or "primitive" groups of plants. Ancient bog formations contained primarily lower forms of plant life, as evidence the Carboniferous period (300 million years) which is commonly referred to as the Age of Ferns or the Coal Age. This lends support to the assumption that the bogs are modern analogues of the ancient coal bogs.

Organic matter originally deposited in a sediment reflects its source material Correlations between the organic compounds found in sediments and the organic compounds present in contemporary organisms have previously been made (Sever, 1970; Douglas *et al.*, 1969; Oro' *et a*l., 1967; Clark and Blumer, 1967). Thus, one may hope to extrapolate from the chemical analyses of certain classes of compounds found in sediments and predict the presence or absence of particular organisms found in their environments of deposition. Sediment samples from the bog were analyzed to confirm such correlations and to determine the relative contributions of the various plants to the bog sediment.

The accumulation of organic matter in these bogs is well preserved. The degree of preservation of organic matter is dependent on the environment of accumulation and early diagenetic changes. Organic material is not washed into the bogs but accumulates at the site of decomposition which is higly reducing. These factors favor preservation of organic matter.

The surface of higher plants is covered with a mixture of lipids referred to as plant waxes. The most common constituents are hydrocarbons, esters, alcohols and acids. The major function of the wax appears to be protection of the plant from water loss and other hazards of the environment (Kolattukudy, 1969). Hydrocarbons are thermally and biologically sufficiently stable to survive geologic time and are thus potentials in geological and paleobioligical investigations. Hydrocarbons are ubiquitous nonetheless minor components in plants and animals (Gerarde and Gerarde, 1962). Terrestrial plant hydrocarbons have a characteristic alkane distribution usually ranging from C25 to C33 with a pronounced odd-carbon-number dominance. It has been suggested that the alkane distribution pattern is a property characteristic of that species, the principal requirement for taxonomic criteria being that it be "species specific" (Eglinton and Hamilton, 1963). Many fatty acids also persist for geologically long periods of time being chemically stable in numerous natural environments. They are major components for most organisms, therefore would be expected to act as "chemical fossils" in sediments. Fatty acid distributions, however, are not as characteristic as alkane distributions; variations in fatty acid composition are observed within a given species due to environmental changes (Shoreland, 1963). Oleic (C18:1) and palmitic (C16:0) acids are the predominant acids in most plant lipids, but many plant fats, usually seed fats, contain unusual or a restricted distribution of fatty acids in high quantities. In general, these restricted acid distributions will be characteristic of genus or of closely-related genera (Lovern, 1965)). To confirm the correlation between geolipids, lipids isolated from geological sources, and

TABLE 1

Bog plants used in chemical analyses

Bryophyta (mosses and liverworts)	
Sphagnum affine R. and C.	*Number 1
Pteridophyta (ferns and clubmosses)	
Lycopodium alopecuroides L.	Number 2
Osmunda cinnamonea L.	Number 3
Pteridium aquilinum (L.) Kuhn	Number 4
Spermatophyta (seed plants)	
Rhynchospera oligantha Gray.	Number 5
Xyris ambigua Beyr.	Number 6
Lachnocaulon anceps (Walt.) Morong.	Number 7
Lachnanthes caroliniana (Lam.) Dandy.	Number 8
Sarracenia psittacina Michx.	Number 9
Drosera rotundifolia L.	Number 10
Drosera filiformis Raf.	Number 11
Rhexia sp (no flowers)	Number 12
Nyssa sylvatica Marsh. var. *biflora* (Walt.) Sarg.	Number 13

* Denotes code name used in Tables 2, 3 and 4.

biolipids, lipids isolated from biological sources, both plants and sediment samples were analyzed and comparisons of fatty acids and hydrocarbons were made.

EXPERIMENTAL

COLLECTION

Both sediments and plants were collected in June, July and August, 1971. June and August are the two major phenological peaks for plant growth (Eleuterius and Jones, 1969). Identification and classification of plants was made by L. N. Eleuterius. (See Table 1 for plant identification). The sediment samples were frozen soon after time of collection and kept frozen until used. All sediment samples were surface samples representing the top 10 cm of sediment. Whole plants including flower (if any) stem and roots were collected, rinsed with distilled water, air dried and then dried in an oven at 40°C for 12 hours. Dried plant material was then pulverized in a Waring blender and re-dried at 40°C for 12 hours to obtain a dry cell weight.

CHEMICAL PROCEDURE AND ANALYTICAL METHODS

EXTRACTION

The frozen sediment was treated with 6N HCl to remove carbonate and washed 5 times with distilled water to remove inorganic salts. After filtering, an aliquot of the mud was removed for total organic carbon analysis. The mud was extracted with methanol/benzene (50:50) using ultrasonic vibrations. The MeOH/benzene was removed by filtration and the mud extracted three times with chloroform using ultrasonic vibrations and stirring. The chloroform and MeOH/benzene extracts were taken to near dryness on a rotary evaporator under reduced pressure. The combined residue was taken to dryness under a stream of filtered nitrogen.

The dried pulverized plant tissue was extracted three times with chloroform using ultrasonic

vibrations. The chloroform extracts were washed with distilled water and the chloroform extracts then taken to near dryness. After transferring the concentrate into a volumetric flask, an aliquot was removed for a lipid weight determination.

SEPARATION

Each lipid sample (plant and sediment) was saponified by refluxing with 0.5N KOH-MeOH for 1 hour. Nonsaponifiable components were removed by extracting the alkaline solution with benzene. Afterwards, the alkaline solution was acidified with dilute HCl to pH 3, and the fatty acids were extracted into benzene. Methyl esters of the fatty acids were prepared using BF_3-MeOH (Metcalf and Schmitz, 1961). Silica Gel (Woelm, Grade 200 Act. I) was packed beneath 25 ml alumina (Woelm Neutral, Grade 100, Act. I) in a 43 cm × 2.5 cm (od) column. The nonsaponifiable residue was fractionated on the column into 4 parts: *n*-hexane fraction contained aliphatic hydrocarbons; benzene fraction contained aromatic hydrocarbons; chloroform-methanol (4:1, v/v) fraction contained alcohols; methanol fraction contained glycerides and the polar lipids.

CHARACTERIZATION

The aliphatic hydrocarbons were identified and measured by gas chromatography on columns of SE-30, Apiezon L, and FFAP (Varian). Standard hydrocarbons were used to calibrate the Perkin-Elmer gas chromatograph 990 equipped with a hydrogen flame ionization detector. The columns were 8 feet by 0.8 inch o.d. copper tubing. The support was 80/100 mesh Chromosorb G, acid washed, dichlorodimethylsilane treated (Johns Mansville). Fatty acid methyl esters were identified using the same instrument but using columns with poly m-phenyl ether (PPE-5 ring), SE-30, and diethylene glycol succinate (DEGS). Linear-log plots of the retention times yielded straight lines for both hydrocarbons and acids and were useful for identification when standards for each carbon number were unavailable. Coinjection of standards were used to clarify some identification. All hydrocarbon samples were run at programmed temperatures from 100° to 260° at 6°C per minute holding at 265°C. All fatty acid methyl esters were run from 150° to 265° at 6°C per minute holding at 265°C. Mass spectra were obtained with a Consolidated Electrotrodynamics Corp., Model 21–110B mass spectrometer. The spectra were run at 70eV.

Additional sample treatment helped in some identifications. Urea adduction (Sever, 1970) enriched the branched from the nonbranched components. Sulfuric acid and/or Bromine-CCl_4 treatment (Morrison and Boyd, 1969) identified unsaturated component peaks.

The organic carbon content of the sediment was determined by a combustion technique using a Leco gasometric carbon analyzer.

RESULTS

The hydrocarbons and fatty acids from plants were assumed to be the main source of the hydrocarbons and fatty acids for the ecosystem studied. Microorganisms are naturally present but their contribution is taken to be small in such an organic-rich sink. Table 2 summarizes the analytical results. The alcohols were chromatogrammed and some alcohols identified. However, a more thorough characterization is in progress and will be reported in the near future thus will not be included in this paper.

The hydrocarbon distribution of the plants, in general, was "typical" for terrestrial plants, that is distribution of normal alkanes fell between C23 and C33 having predominant odd-carbon preferences (see Table 3). However, *Drosera sp.* (No. 11) commonly known as the Sundew plant, contained C17 as a major constituent in its hydrocarbon components (see Figure 2). This is significant since alkanes of carbon number less than C23 and more than C35 are rarely present in

TABLE 2

Analytical analyses of Bog plants and sediment

Plant number	1	2	3	4	5	6	7
Lipid weight (grams)	0.944	10.19	2.170	1.319	1.152	1.090	2.400
Dry cell weight	100.0	80.43	70.74	100.0	98.44	85.90	56.41
Hydrocarbon weight	0.0112	0.0106	0.0099	0.0039	0.0099	0.006	0.028
Benzene fraction (aromatic hydrocarbons) wt.	0.443	0.410	0.270	0.0266	0.0047	0.059	....
Alcohol fraction wt.	0.0053	0.0059	0.0049	0.0305	0.0268	0.00006	0.0969
MeOH fraction (polar lipid) wt.	0.0053	0.032	0.0209	0.0120	0.0195	0.0077	0.0008
Fatty acid methyl ester wt.	0.162	0.661	0.250	0.0084	0.0201	0.045	0.1606
Percent hydrocarbon/dry cell wt.	0.0111	0.0132	0.0147	0.0039	0.0105	0.0074	0.0261
Percent alcohol/dry cell wt.	0.0024	0.0074	0.0069	0.0305	0.0286	0.0001	0.172
Percent FAME/dry cell wt.	0.161	0.822	0.372	0.0084	0.0217	0.047	0.285
Percent hydrocarbon/ lipid wt.	1.19	0.104	0.480	0.257	0.903	0.578	0.612
Percent alcohol/lipid wt.	0.258	0.0583	0.226	2.31	2.44	0.0055	4.04
Percent FAME/lipid wt.	17.2	6.49	12.1	0.637	1.83	3.67	6.69
Percent lipid/dry cell wt.	0.937	12.7	3.07	1.32	1.70	1.27	4.25

Plant number	8	9	10	11	12	13	Sediment
Lipid weight (grams)	5.49	1.94	1.105	4.298	0.374	20.16	5.514
Dry cell weight	158.3	55.32	30.11	79.38	100.7	190.4	788.4
Hydrocarbon weight	0.0247	0.0208	0.0040	0.028	0.0084	0.6063	0.0265
Benzene fraction (aromatic hydrocarbons) wt.	0.309	0.0897	0.0266	0.0609	0.0192	0.9481	0.0425
Alcohol fraction wt.	0.0145	0.00491	0.00217	0.0608	0.0435	0.4994	0.0803
MeOH fraction (polar lipid) wt.	0.0078	0.0344	0.0115	0.072	0.0149	0.0116	0.023
Fatty acid methyl ester wt.	0.7156	0.0802	0.00841	0.4003	0.222	0.0926	0.5515
Percent hydrocarbon/dry cell wt.	0.016	0.0396	0.0134	0.0354	0.0087	0.318	0.0036
Percent alcohol/dry cell wt.	0.009	0.0089	0.0072	0.0767	0.0454	0.0262	0.0107
Percent FAME dry cell wt.	0.452	0.145	0.028	0.504	0.232	0.0486	0.074
Percent hydrocarbon/ lipid wt.	0.450	1.07	0.366	0.654	2.34	3.01	0.050
Percent alcohol/lipid wt.	0.264	0.252	0.196	1.42	12. 2	0.248	1.54
Percent FAME/lipid wt.	13.0	4.13	0.760	9.31	62.5	0.459	10.5
Percent lipid/dry cell wt.	3.47	3.51	3.67	5.41	0.371	10.62	0.78

higher plants to any appreciable extent. However, C17 is the major hydrocarbon component most often identified in blue-green algae (Winters *et al.*, 1969; *Gelpi et al.*, 1970). Several plants, *Drosera sp.* (No. 11), *Lycopodium sp.* (No. 2), and *Osmunda sp.* (No. 3) (flowering plant, clubmoss, and fern), contained C28 as a major hydrocarbon component. This is very unusual since it is rare that an even-numbered carbon is a major hydrocarbon component though there have been reports of organisms containing even-numbered carbon predominances (Cocker and Shaw, 1963; Stevenson, 1961). The major component C28 was con-

firmed by mass-spectrometric analysis. *Nyssa sylvatica* (No. 13) commonly known as Black Gum, Water-tupelo, or Water-Gum contained one dominant hydrocarbon, C31. This hydrocarbon represented more than 90% of the total aliphatic hydrocarbon fraction. This species apparently makes a large contribution to the extractable organic matter in the bog since the percent lipid extractable from this plant is extremely high (10.6%). In addition to the homologous series of *n*-alkalanes, we recorded the presence of another homologous series in *Sarracenia psittacina* (No. 9) and *Lachnanthes caroliniana* (No. 8). This series is formed by hydrocarbons of another type, most likely the series is *iso-* or *anteiso-*alkanes. Because these long chain hydrocarbons are easily adducted with urea,

TABLE 3

Percent composition of normal hydrocarbons in Bog plants and sediment

Hydrocarbon	Plant 1	2	3	4	5	6	7
17:0	0.60	..	..	..	tr	1.46	0.87
18:0	tr	..	4.78	6.28	tr	1.62	0.72
19:0	tr	..	tr	4.89	2.66	1.17	0.90
20:0	tr	..	..	5.58	..	0.90	0.79
21:0	7.77	..	tr	3.66	6.50	7.25	0.64
22:0	tr	..	2.43	5.50	..	1.72	0.64
23:0	1.94	..	2.09	8.38	3.52	18.57	1.15
24:0	1.04	..	2.43	6.28	..	2.84	0.87
25:0	4.56	2.39	5.68	25.04	1.99	25.61	1.41
26:0	1.71	..	4.11	6.11	1.60	2.03	1.23
27:0	2.21	4.14	10.42	15.71	3.48	10.69	6.73
28:0	3.11	76.63	16.06	3.49	17.42	2.14	1.54
29:0	10.37	2.39	17.33	9.08	16.53	8.22	10.42
30:0	3.80	..	4.03	..	4.26	1.98	1.35
31:0	40.84	1.33	6.39	..	8.45	5.74	56.15
32:0	1.57	..	4.93	..	..	0.68	1.28
33:0	2.94	13.12	tr	..	4.30	..	..

Hydrocarbon	Plant 8	9	10	11	12	13	Sediment
17:0	..	2.15	20.09	0.40	4.82	..	2.71
18:0	..	2.84	4.94	..	3.35	..	0.89
19:0	..	1.01	tr	0.41	2.96	..	1.78
20:0	..	0.73	tr	..	1.58	..	0.89
21:0	5.87	0.73	1.61	1.16	4.31	..	2.16
22:0	1.55	1.03	1.74	0.60	1.77	..	1.43
23:0	19.54	2.48	3.33	20.10	7.18	..	3.55
24:0	2.00	2.29	2.41	2.01	2.62	..	2.28
25:0	13.08	4.86	5.97	23.52	5.32	..	7.17
26:0	0.78	4.01	3.48	1.34	2.62	..	2.48
27:0	6.73	8.05	12.86	6.97	6.90	..	10.57
28:0	2.61	9.90	4.02	33.0	4.17	1.69	2.86
29:0	23.54	15.89	14.92	3.02	13.18	3.55	14.34
30:0	1.47	9.28	2.41	0.30	5.45	1.91	3.04
31:0	14.35	11.35	11.92	1.81	16.66	91.34	16.44
32:0	..	2.57	..	..	1.65	0.51	1.90
33:0	0.47	6.90	1.61	..	5.73	..	6.03

branching in the middle of the chain was ruled out. However, because of the lack of standards and the very small concentration in the series, they were not further characterized. Combined gas chromatographic-mass spectrometric data will be obtained on these homologous series later.

The hydrocarbon concentrations in the plants ranged from 70 to 3,000 ppm based on dry cell weight, *Nyssa sylvatica* having the highest concentration. These numbers present minimum concentrations because the efficiency of hydrocarbon extraction is not known.

The alkane distribution in the sediment samples ranged from C14 to C33 with a maximum at C31 (see Figure 3), and a predominance of hydrocarbons having odd-numbered-carbons is evident, thus reflecting the distributions of the plant alkanes. There appears to be no significant amount of C28 in the sediment alkanes, therefore the plants containing this particular alkane must not be a major contribution to the bog sediment. The very limited abundances of the plants containing C28 supports this conclusion. Hydrocarbon concentration in the sediment was 36 ppm. This is on the order of two magnitudes less than the average plant hydrocarbon concentration. The extractable lipid materal from the sediment was less than 1% whereas the total organic matter was 20.0%. The 95% not extracted represents insoluble organic carbon called kerogen (Forsman and Hunt, 1958).

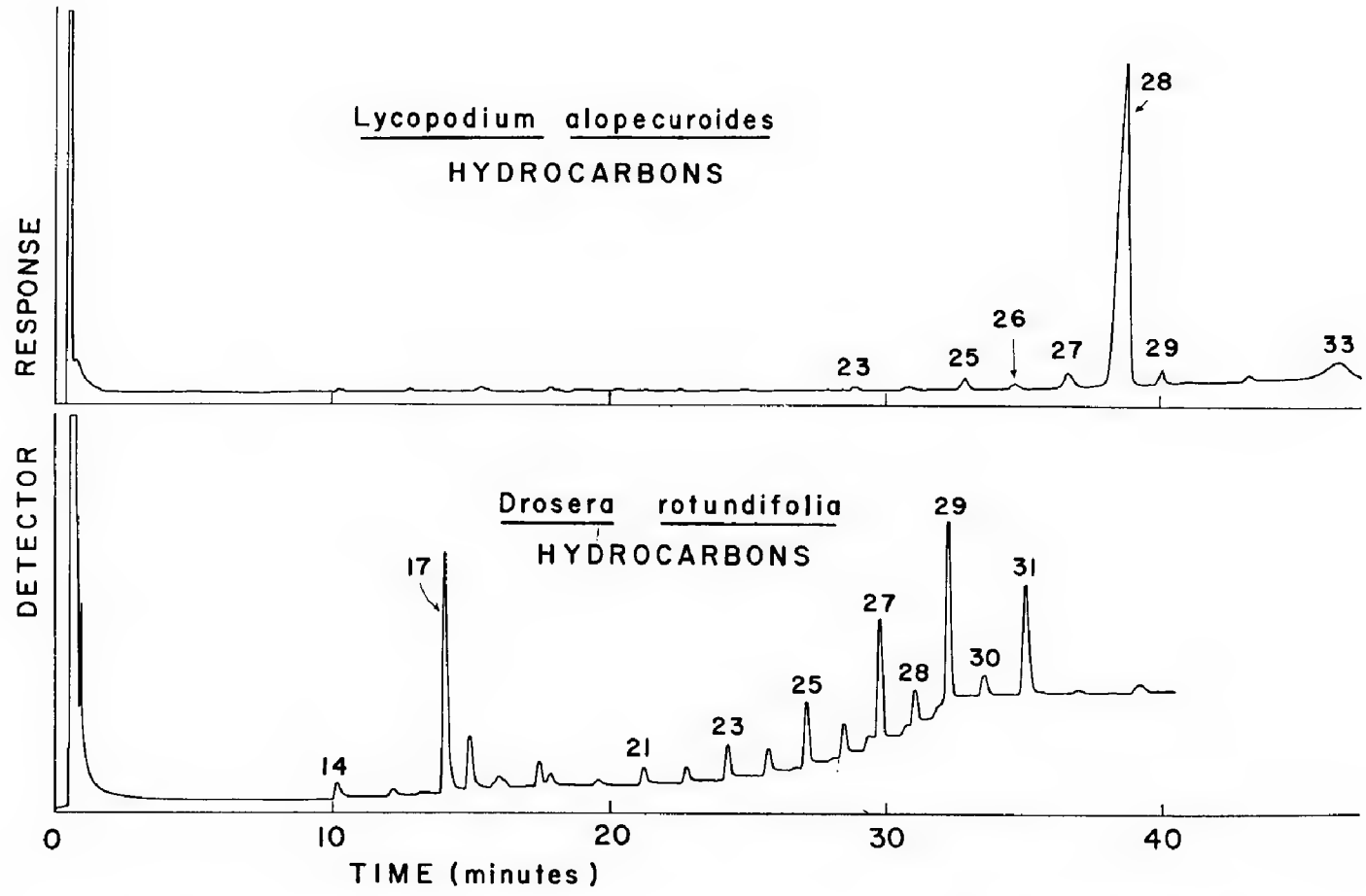

FIG. 2. Top: Gas chromatogram of total hydrocarbons of *Lycopodium alopecuroides*. Perkin-Elmer Model 990 gas chromatograph with helium flow at 25 ml/min. Temperature programmed from 100°C to 260°C at 6°C/min. Copper column (8 ft. × 0.8, o.d.) packed with 5% FFAP on Varaport 30. Bottom: Gas chromatogram of total hydrocarbons of *Drosera rotundifolia*. Perkin-Elmer Model 990 gas chromatograph with helium flow at 25 ml/min. Temperature programmed from 100°C to 260°C at 6°C/min. Copper column (8 ft. × 0.8, o.d.) packed with 3% SE-30 on Chromosorb G.

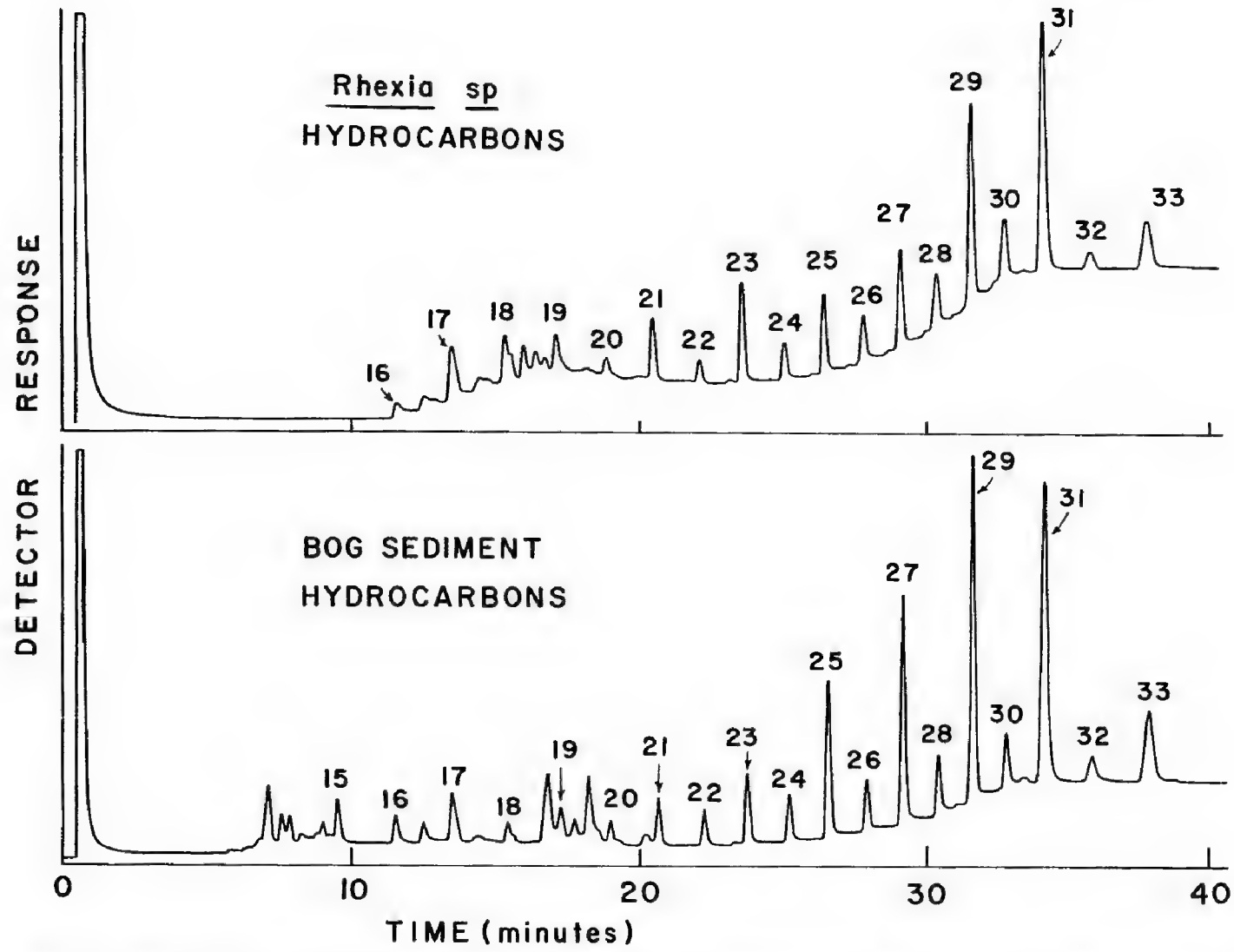

FIG. 3. Top: Gas chromatogram of total hydrocarbons of *Rhexia sp.* Bottom: Gas chromatogram of total hydrocarbons of Bog Sediment. Conditions for both chromatograms were the same. Perkin-Elmer Model 990 gas chromatograph with a helium flow rate of 25 ml/min. Temperature programmed from 100°C to 260°C at 6°C/min. Copper column (8 ft. × 0.8 inches, o.d.) packed with 3% SE-30 on Chromosorb G.

A small percent (less than 5%) of the hydrocarbon fraction in the sediment represented olefinic material. However, the plants also had a low concentration of olefinic hydrocarbons. Traces of pristane were recognizable by enrichment in the nonadductus of urea clathration products and also by relative retention times as compared to a standard.

The fatty acid distributions ranged from C12:0 to C28:0 in the bog plants (see Table 4). Finding higher molecular weight fatty acids came somewhat as a surprise since linolenic (C18:3) is the major fatty acid constituent in leaf lipids (Hilditch, 1956), and distributions usually range from C12:0 to C18:3. Many of the fatty acids in the high molecular weight region of the chromatograms were not identified. Further characterization is in progress. The fatty acids found in roots and seeds of plants are different from leaf distributions (Shoreland, 1963) and could account for some of the higher molecular weight fatty acids isolated. In all samples there was a pronounced even-carbon-number preference.

The fatty acid concentrations found in the plants ranged from 80 to 8,200 ppm with an average of 3,000 ppm whereas the sediment fatty acids were only 700 ppm.

Correlation of sediment and plant fatty acids seems evident when one notes

the similartity of distributions of the fatty acids in the sediment and in most of the plants (see Table 4).

CONCLUSIONS

Most of the plants growing in the bog environment had typical terrestrial plant hydrocarbon and fatty acid distributions. However, some of the plants appear to have unique distributions of both fatty acids and hydrocarbons. Because the bog contained plants representative of different stages of evolutionary development, it would be interesting to correlate molecular complexities of each species with their evolutionary development. However, because caution has been advised since phylogenetic comparisons are only justifiable within limited taxonic groupings (Gelpi *et al.*, 1970; Blumer *et al.*, 1971), and because of our limited data on the plants harvested at different growth stages, we only site interesting observations at this time.

1. *Spahgnum* (moss) contained wider ranges of both hydrocarbons and fatty acids than would be expected. Several of the lower plants showed substantial amounts of higher fatty acids which appears to be an interesting area to explore further since these ranges for fatty acids in plants have not before been reported. (Interestingly, one plant not reported, *Sarracenia alata*, from initial studies seems to have a distribution of even-carbon numbered fatty acids from C12:0 to C30:0 roughly approximating the distribution of odd-carbon numbered hydrocarbons from C13:0 to C31:0).
2. *Lycopodium* (clubmoss) contained predominantly C28 hydrocarbon, seventy-seven percent of the aliphatic hydrocarbon content. Hydrocarbon preference for even-carbon numbers in organisms is rare.
3. *Osmunda* (fern) contained as the second most abundant hydrocarbon, C28 *n*-alkane.
4. *Drosera rotundifolia* (flowering plant) also contained a large percentage of C28 *n*-alkane in the aliphatic hydrocarbon fraction.
5. *Nyssa* (flowering plant) contained almost exclusively C31 *n*-alkane in the hydrocarbon fraction.

If a mass balance of productivity of plant species is approximated over several seasons so that estimations of the relative contributions of organic matter of each plant to the sediment can be made, then correlations can be made between sediment and plant hydrocarbons and sediment and plant fatty acids. Assuming that the seed plants are the principal contributors of hydrocarbons, which is attested to by their greater abundance in the bog as well as their generally higher concentrations of total hydrocarbons, the distribution of hydrocarbons in the sediemnt mirrors well the distribution achieved in a simulated mixture of dry cell weights of the seed plants, i.e. a pronounced odd-carbon predominance in the region of C17-C33 with a maximum at C31. This simulated mixture of plants, however, would not account for the distribution of fatty acids in the sediments. The generally higher percentages of fatty acids in the lower plants may in part account for the presence of higher fatty acids in the sediment.

In this approach to implicate plants of a specific environment as the source of

TABLE 4

Percent composition of normal fatty acids in Bog plants and sediment

Fatty acid	Plant 1	2	3	4	5	6	7
12:0	0.95	3.29	..	..	..	..	0.66
12:0	1.19	9.61	..	..	..	..	..
13:0	..	..	..	..	..	..	..
14:0	0.88	..	0.30	..	..	..	0.84
15:0	tr	..	..	..	..	..	..
16:0	tr	..	2.35	20.22	14.07	3.12	..
16:1	16.02	20.14	26.01	..	..	24.62	19.46
16:2	2.27	6.18	..	..	..	..	..
18:0	2.73	2.10	6.60	9.53	8.34	11.61	2.20
18:1	29.68	41.59	..	1.11	3.05	..	73.87
18:2	..	..	..	..	..	..	..
20:0	..	..	..	19.95	11.39	..	0.60
21:0	..	..	..	..	2.61	..	..
22:0	..	..	..	14.07	13.83	..	..
23:0	..	..	..	2.07	4.03	..	..
24:0	..		..	21.27	17.36	..	..
25:0	..	..	..	..	5.19	..	..
26:0	..	.	..	6.35	12.61	..	..
27:0	..	..	..	..	..	..	..
28:0	..	.	..	..	7.32	..	..

Fatty acid	Plant 8	9	10	11	12	13	Sediment
12:0	3.07	..	..	1.37	6.70	13.31	..
12:1	..	..	..	..	..	..	..
13:0	..	..	..	..	..	7.71	..
14:0	1.73	1.69	..	3.11	1.94	4.51	..
15:0	0.46	..	..	..	..	3.51	..
16:0	2.41	1.59	23.7	38.75	42.62	2.34	5.2
16:1	23.13	29.41	..	..	..	..	..
16:2	..	..	..	..	..	..	..
18:0	5.92	4.62	2.44	8.23	18.40	12.15	2.6
18:1	55.63	60.13	3.71	2.74	17.92	..	2.4
18:2	..	..	..	..	..	..	..
20:0	1.27	..	3.61	9.88	3.87	..	4.2
21:0	..	..	..	..	..	..	..
22:0	..	..	9.08	17.29	1.61	..	9.2
23:0	.	..	1.95	..	..	..	3.4
24:0	..	..	22.4	13.77	1.13	..	19.4
25:0	..	..	4.10	..	..	..	5.2
26:0	..	..	15.4	4.94	..	..	27.2
27:0	..	..	0.57	..	..	..	3.7
28:0	..	..	10.6	..	..	..	15.0

organic compounds, specifically hydrocarbons and fatty acids, found in sediments, good correlations were noted for sediment and plant hydrocarbons and fatty acids. Organic geochemists may be aided in their interpretations of sedimentary organic matter.

ACKNOWLEDGMENTS

The work was supported in part by the donors of The Petroleum Research Fund, administered by The American Chemical Society. The technical assistance of Miss Ginny Moyer and Mr. Lee Howell is gratefully acknowledged. We also thank Mr. Rashwan Hassan for mass spectra data and Mr. L. N. Eleuterius for plant identification and classification. Various parts of the investigation were carried out at Rice University (Houston, Texas), the Gulf Coast Research Laboratory (Ocean Springs, Mississippi), and Louisiana State University (Baton Rouge, Louisiana).

LITERATURE CITED

BLUMER, M., R. R. GUILLARD and T. CHASE. 1971. Hydrocarbons of Marine Plankton. *Mar. Biol.* **8:** 183–189.

CLARK, R. C. and M. BLUMER. 1967. Distribution of *n*-Paraffins in Marine Organisms and Sediments. *Limnol. Oceanog.* **12:** 79–87.

COCKER, W. and R. E. A. SHAW. 1963. Extractices from *Manikana bidentata. J. chem. Soc.* **1963:** 677–680.

DOUGLAS, A. G., G. EGLINTON, and J. R. MAXWELL. 1969. The hydrocarbons of Coorongite. *Geochim. cosmochim. Acta.* **33:** 569–577.

EGLINTON, G. and R. J. HAMILTON. 1963. Distribution of Alkanes. In *Chemical Plant Taxonomy*, T. Swain (ed.) Academic Press, Inc., New York.

ELEUTERIUS, L. N. and S. B. JONES, JR. 1969. A Floristic and Ecological Study of Pitcher Plant Bogs in South Mississippi. *Rhodora.* **71:** 785–790.

ELEUTERIUS, L. N. 1968. Floristics and Ecology of Coastal Bogs in Mississippi. M.S. thesis. University of Southern Mississippi, Hattiesburg, 1968.

FORSMAN, J. P. and J. M. HUNT. 1958. Insoluble organic matter (Kerogen) in Sedimentary rocks of marine origin. In *Habitat of Oil*, L. G. Weeks (ed.) Am. Assoc. Petrol. Geol., Tulsa, Oklahoma.

GELPI, E. H. SCHNEIDER, J. MANN and J. ORO'. 1970. Hydrocarbons of Geochemical Significance. *Phytochemistry.* **9:** 603–612.

GERARDE, H. W. and D. F. GERARDE. 1962. The ubiquitous hydrocarbons. Association of Food and Drug Officials of the United States. Vol. **26.**

HILDITCH, T. P. 1956. In *The Chemical Constitution of Natural Fats*, 3rd Ed. Chapman and Hall, London.

KOLATTUKUDY, P. E. 1969. Plant Waxes. *Lipids* **5:** 259–275.

LOVERN, J. A. Neutral Fats and Oils. 1965. In *Comprehensive Biochemistry*, Florkin and Stotz (eds.) **6:** 52–82. Elsevier Publishing Company, New York.

METCALF, L. D. and A. A. SCHMITZ. 1961. The Rapid preparation of Fatty Acid Esters for gas chromatographic analysis. *Analyt. Chem.* **33:** 363–364.

MORRISON, T. R. and R. N. BOYD. 1969. In *Organic Chemistry*, 2nd Ed. Allyn and Bacon, Inc., Boston.

ORO', J., T. G. TORNABENE, D. W. NOONER, and E. GELPI. 1967. Aliphatic Hydrocarbons and Fatty Acids of Some Marine and Freshwater Microorganisms. *J. Bact.* **93:** 1811–1820.

SEVER, J. R. 1970. Organic Geochemistry of Hydrocarbons in Coastal Environments. Ph.D. Dissertation, The University of Texas at Austin.

SHORELAND, F. B. 1963. Distribution of fatty acids in plant Lipids. In *Chemical Plant Taxonomy*, T. Swain (ed.) Academic Press, Inc., New York.

STEVENSON, R. 1961. Some Constituents of *Calendula officinalis*. *J. org. Chem.* **26:** 5228–5230.

WINTERS, K., P. L. PARKER, and CHASE VAN BAALEN. 1969. Hydrocarbons of Blue-Green Algae: Geochemical Significance. *Science* **158:** 467–468.

MARSH PRODUCTION: A SUMMARY OF THE LITERATURE

Carolyn W. Keefe

Chesapeake Biological Laboratory, Natural Resources Institute, University of Maryland, Solomons, Maryland 20688

Contribution No. 483, Natural Resources Institute, University of Maryland

ABSTRACT

A review has been made of studies of freshwater and saltwater marsh production. Reasons are discussed for the unusually high produciton of these communities when compared with terrestrial communities and phytoplankton. The role of marsh plants as food for consumers is also discussed.

INTRODUCTION

It has long been recognized that primary production of marshes is high when compared with the production of terrestrial communities (Odum, 1959). There have been many reasons offered to explain this high production. The purpose of this paper is to summarize the studies made of marsh primary production.

PRODUCTION MEASUREMENTS

Primary production of angiosperms in marshes is usually measured by harvesting. Since marsh plants show a marked annual fluctuation in biomass, production can be estimated by measuring increase in biomass during the growing season. Production is defined as the change in biomass of the entire plant over time.

Because of the difficulty of sampling root material, most investigators have measured production of only aerial portions. Basically, this is done in one of two ways:

1. At intervals through the growing season, aerials are clipped in a unit area selected at random from a larger area. Living and dead components are separated. Production is calculated from the total of the increases in material as indicated by weighing. [Production $= \Sigma(\Delta\text{living} + \Delta\text{dead})$].
2. At the peak of the growing season, aerials are clipped in a unit area selected at random from a larger area. Only the living material is collected and the weight of an average mature leaf is determined. Estimates are made from leaf scars and damaged leaves of the amount of material that died or was otherwise removed before harvest. Production is calculated from the weight of the material present plus material that the investigator estimates was removed prior to harvest (Williams and Murdoch, 1969).

Underground production of root material can be measured in approximately the same way as Method 1 for aerial production. The cumulative change in biomass of the underground parts is measured through the year. The point in time at which the total matter produced aerially and underground is greatest represents time of maximum production for the year. There are basically two methods for obtaining the change in underground biomass.

1. Underground parts of individual plants are washed of the excess non-living material, then dried and weighed. From the amount of root material per plant, the amount of underground living material in the quadrat is determined.
2. Cores are taken throughout the quadrat. Living and dead material are separated, then dried and weighed. From the amount of root material per core, the amount of underground living material in the quadrat is determined.

Method 1 tends to underestimate the amount of mass present, while Method 2 tends to overestimate the material. A simpler method is to measure the shoot:root ratio on one sampling day, then extrapolate total production from aerial production. However, this can be inaccurate since translocation causes the shoot:root ratio to vary through the year (Jervis, 1964; Westlake, 1965).

An inspection of Table 1 shows how frequently production of *Spartina* and *Typha* has been measured. Total production of *Spartina* has not been measured, since it is difficult to distinguish past underground growth from present. Smalley (1959) found a 1:1 ratio of all roots and rhizomes to green leaves. *Spartina* peat is quite matted so the roots and rhizomes are not easily separated from the entrapped clay and other inorganic constituents. On the marsh adge, this mat withstands storms well, helping to maintain the marsh and causing entrapment of waterborne particles to expand the marsh area. Underground production of *Typha* is much easier to measure, since the living rhizomes can be asily differentiated from the dead by the white, healthy appearance of living cross-sections (Jervis, 1964).

These estimates of total production are estimates of net primary production. Since there are few studies in which both net production and respiration have been measured, only a few estimates of gross production are available (gross production = net production + respiration). Bray (1962) estimated net production to be 85% of gross in a *Typha angustifolia-latifolia* hybrid community in Minnesota. Teal and Kanwisher (1966) measured respiration of *Spartina alterniflora* in Georgia and found that net production (Smalley, 1959, 1960) amounts to 23% of gross. The difference in respiration between *Typha* and *Spartina* may be due to different habitats and climates, as well as different methods of measurement.

Net production is expressed as increase in weight (wet weight, dry weight, ash-free dry weight, or carbon weight). Wet weight is easiest to measure but somewhat variable, depending on environmental conditions experienced by the plant before harvest and its treatment before weighing. Since weight loss during drying varies from 5–95%, dry weight is a more precise basis for calculating production. Dry weight is measured after drying to constant weight at 60° or 104–

TABLE 1

Summary of biomass and production values for marsh plants

Species	Biomass-g(dry)/m²			Net production g(dry)/m²/yr		Locale	Source
	Underground parts	Aerial parts	Total	Aerial	Total		
Spartina alterniflora	....	....	....	973	....	Georgia	Smalley (1959)
	....	....	....	2000–3300	....	Georgia	Odum (1959, 1961)
	....	259–1320	....	329–1296	....	North Carolina	Stroud & Cooper (1969)
	....	545	....	650	....	North Carolina	Williams & Murdoch (1969)
	....	250–2100	....	1000	....	North Carolina	Williams & Murdoch (1966)
	....	1332	....	....	....	Virginia	Wass & Wright (1969)
	....	413	....	445	....	Delaware	Morgan (1961)
	....	300	....	....	....	New Jersey	Good (1965)
Spartina patens	....	640	....	1296	....	North Carolina	Waits (1967)
	....	805	....	....	....	Virginia	Wass & Wright (1969)
	....	....	....	993	....	Long Island	Harper (1918)
Spartina cynosuroides	....	1456	....	....	....	Virginia	Wass & Wright (1969)
Spartina townsendii	...	700–1060	....	....	....	So. England	Ranwell (1961, 1964b)
Distichlis spicata	....	360	....	....	....	Virginia	Wass & Wright (1969)
Fimbristylis	....	605	....	....	....	Virginia	Wass & Wright (1969)
Borrichia	....	785	....	....	....	Virginia	Wass & Wright (1969)
Phragmites communis	....	....	....	2695	....	Long Island	Harper (1918)
	....	1000	....	....	....	England	Pearsall & Gorham (1956)
	.. .	497	....	....	....	England	Buttery & Lambert (1965)
	....	3650	....	....	....	Sweden	Stake (1967)

TABLE 1—Continued

Summary of biomass and production values for marsh plants

Species	Biomass-g(dry)/m²			Net production g(dry)/m²/yr		Locale	Source
	Underground parts	Aerial parts	Total	Aerial	Total		
Juncus roemerianus	....	232	....	849	....	Florida	Heald (1969)
	....	....	...	560	....	North Carolina	Foster (1968)
	....	1173	....	796	....	North Carolina	Stroud & Cooper (1969)
	....	786	....	1360	....	North Carolina	Waits (1967)
	....	340	....	850	....	North Carolina	Williams & Murdoch (1968)
	....	650	....	....	....	Virginia	Wass & Wright (1969)
Juncus effusus	....	800	....	....	....	England	Pearsall & Gorham (1956)
Juncus squarrosus	....	690	....	....	....	England	Pearsall & Gorham (1956)
Atriplex hastata	....	700–800	....	....	....	So. England	Ranwell (1961)
Scirpus lacustris (cultivated)	....	1000	....	6400	....	Germany	Seidel (1959)
Scirpus americana	....	150	....	150	....	So. Carolina	Boyd (1970b)
Typha latifolia	....	684	....	684	....	So. Carolina	Boyd (1970b)
	....	1527	....	....	....	Oklahoma	Penfound (1956)
	....	....	....	1358	....	Long Island	Harper (1918)
	....	1070	....	....	....	England	Pearsall & Gorham (1956)
	....	60	....	....	....	England	Buttery & Lambert (1965)
	912	404	1316	....	....	No. Dakota	McNaughton (1966)
	556	416	972	....	....	Nebraska	McNaughton (1966)
Typha angustifolia	....	930	....	....	....	Virginia	Wass & Wright (1969)
	....	....	....	1733	....	Long Island	Harper (1918)
Typha latifolia-angustifolia (hybrid)	2960	1360	4320	1360	1360	Minnesota	Bray (1962)

TABLE 1—Continued

Summary of biomass and production values for marsh plants

Species	Biomass-g(dry)/m²			Net production g(dry)/m²/yr		Locale	Source
	Underground parts	Aerial parts	Total	Aerial	Total		
Typha latifolia and *T. angustifolia* community	1800	1380	3180	1905	3205	New Jersey	Jervis (1964)
	892	378	1250	....	....	So. Dakota	McNaughton (1966)
Typha latifolia and *T. domingensis* community	804	730	1534	....	....	Oklahoma	McNaughton (1966)
	2646	1336	3982	....	....	Texas	McNaughton (1966)
Zizania aquatica	....	560	....	....	....	Virginia	Wass & Wright (1969)
	....	1200	....	1547	....	New Jersey	Jervis (1964)
	50	500	550	....	....	Minnesota	Bray *et al.* (1959)
Carex stricta	....	1340	....	1699	....	New Jersey	Jervis (1964)
Carex spp.	....	400–630	....	....	....	England	Pearsall & Gorham (1956)
Carex rostrata	....	136–370	....	....	....	Lappland	Pearsall & Newbould (1957)
Butomus umbellatus	....	2000	....	....	....	Sweden	Stake (1967)
Sparganium ramosum	....	2530	....	....	....	Sweden	Stake (1967)
Leersia oryzoides	....	1545	....	....	....	Virginia	Wass & Wright (1969)
Nuphar advena	....	245	....	....	....	Virginia	Wass & Wright (1969)
Eichhornia crassipes	....	1478	....	....	....	Louisiana	Penfound & Earle (1948)
	....	1276	....	....	....	Louisiana	Penfound (1956)
Justicia americana	1818	640	2458	247	....	Alabama	Boyd (1969)
Alternanthera philoxeroides	....	841	....	....	....	Alabama	Boyd (1969)
Glyceria maxima	1520	656	2176	....	....	England	Westlake (1966)
	....	998	....	....	....	England	Buttery & Lambert (1965)

105°C. Ash-free dry weight measures only the organic material present and is, therefore, an excellent weight for determination of production. The quantity of ash remaining after combustion at 550°C is subtracted from the dry weight to obtain ash-free dry weight. Ash-free dry weight has the advantage of eliminating calcareous compounds present in plants. If not removed, these compounds would give "false-high" values of material produced. Weight of carbon is closely related to ash-free dry weight since most organic matter is approximately 45% carbon. Carbon content provides an index of the organic matter produced. However, measure of carbon weight ignores the other components of the organic matter. For this reason, estimates of production based on ash-free dry weights are the best indications of the amount of organic matter available to the consumers.

FACTORS INFLUENCING MARSH PRODUCTION

Table 1 gives biomass and production values for a variety of marsh plants. For those species for which several production estimates have been made, there is generally a decrease in production from south to north. *Spartina* exhibits this pattern particularly well (Figure 1).

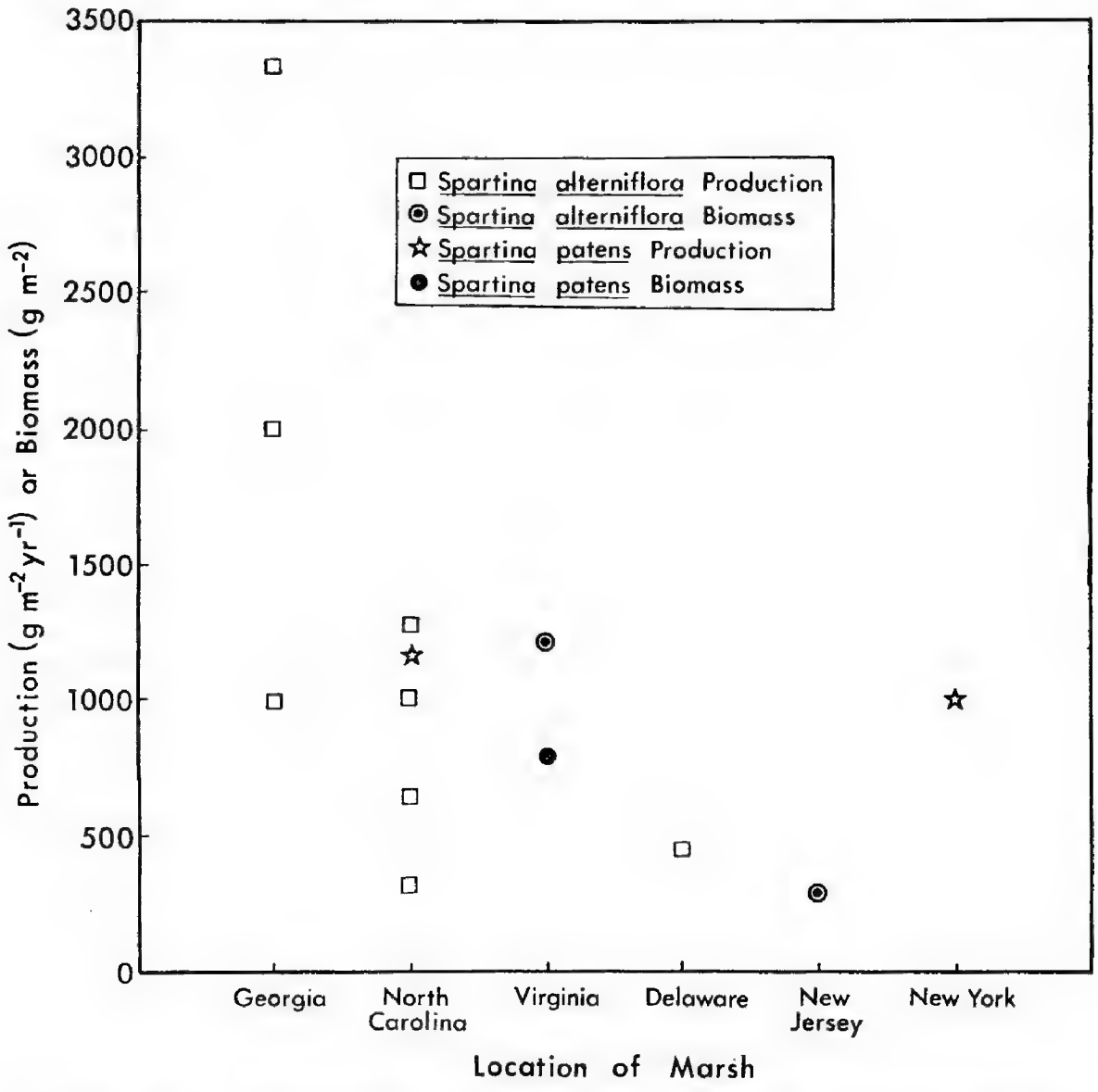

FIG. 1. Comparison of production and biomass estimates of *Spartina alterniflora* and *Spartina patens* in Atlantic Coast marshes. The results of several separate studies in Georgia and North Carolina are shown individually.

The high production of marsh vegetation in comparison with other plants (Odum, 1959; Westlake, 1963) has been attributed to a variety of factors. The growing season in marshes is generally longer than for cultivated crops. The rather hostile environment of the anaerobic marsh soil has been adapted to by the plants (Laing, 1940a, b). High salinities (40–50 ppt) can be tolerated by *Spartina alterniflora* (Hoese, 1967), although it germinates best in fresh water. It is able to compete for growth space best in saline marshes (Teal and Teal, 1969), and even able to tolerate oil spills there (Baker, 1970).

The high production of *Typha latifolia-angustifolia* hybrid has been partially attributed to hybrid vigor (Bray, Lawrence and Pearson, 1959). The same may be true of *Spartina townsendii*, a hybrid of *S. alterniflora* and *S. maritima*. This species was discovered in 1870 and has extended over thousands of acres of previously unvegetated English and French coasts (Hubbard, 1969).

A less obvious reason for high marsh production relative to terrestrial production is the vertical orientation of the leaves of most marsh plants. This reduces intense heating (Palmer, 1941), exposes the maximum leaf surface to sunlight over the day, and minimizes mutual shading (Jervis, 1964). Leaf orientation can be quantified by using the leaf area index. This is the ratio of leaf area to the area of the ground underneath (e.g., cm^2 leaf surface:cm^2 ground). Leaf area indices for field crops under normal cultivation range from 2 to 3 and occasionally 4 (Pearsall, 1954). Maximum production of sugar beet crops occurs when the index is 6 to 9. For kale, maximum production is at an index of 3. When the index is higher than this, mutual shading occurs, so production drops (Watson, 1958). The average leaf area index for a New Jersey freshwater marsh is 15.4 (Jervis, 1964). Whether this index is high enough to cause shading and limit production per unit area is not known.

Abundant soil water undoubtedly plays an important role in maintaining high productivity. The water is used directly by the plants and also holds the nutrients in a dissolved state in the sediments. Under drought conditions, nutrients may be precipitated and no longer immediately available to the plants (Gooch, 1968). During a drought in New Jersey, the water table dropped, but the peat retained its water, allowing the marsh plants to continue to grow (Jervis, 1964).

The high nutrient content of marsh soils and water also helps maintain high productivity. The tide moves nutrients from external sources onto salt marshes (Aurand, 1968). Also, other factors being equal, flowing water is more productive than standing water (Schelske and Odum, 1961). Particles rich in nutrients are trapped on the marsh by obstructions provided by the plants (Gorham and Pearsall, 1956; Blum, 1969; Ranwell, 1964a), thus increasing the size of the marsh laterally and vertically, while providing soil rich in nutrients for the plants. Ranwell (1964b), working in a rapidly expanding *Spartina townsendii* marsh on the seacoast, reported that soil nutrients decreased in concentration away from the sea (the source of the sediment). Near the sea, the sediment contained 0.11% phosphorus and 0.30% nitrogen. Near the landward edge of the marsh, the sediment contained 0.07% phosphorus and 0.11% nitrogen, indicating that nutrients for the plants were derived from the next most seaward loca-

tion. These plants could be nutrient limited if there were no replenishment by the nutrient-rich sediments deposited there by the sea.

Pomeroy, Johannes, Odum, and Roffman (1969) have found that the sediment in the well-established coastal *Spartina alterniflora* marsh they studied contained enough phosphorus for 500 years growth without replenishment by additional input or recycling on the marsh. Their P^{32} studies indicate that *Spartina* obtains its phosphorus from the soil. The phosphorus in the water provides phosphorus for the sediment since it is rapidly sorbed on the surface of the sediment, then combined into the crystal lattice of the clay. From this combination with the clay, it can still be released as free phosphate available for biological uptake (Pomeroy, Smith, and Grant, 1965). Thus, the large supply of phosphorus in the sediment assures a continuing source of phosphorus for phytoplankton and mud algae, as well as for *Spartina*.

Nutrient levels in the water over freshwater marshes are often high. Buttery, Williams, and Lamber (1965) reported values of 0.17–0.30 mg PO_4-P liter^{-1}, 0.81–1.18 mg NO_3-N liter^{-1} and 2.88–1.08 mg NH_3-N liter^{-1} in the water over a *Phragmites communis-Glyceria maxima* streamside marsh. Nitrogen in the soil water varied from 48.3–110.0 mg liter^{-1}. Phosphorus in the soil water decreased from 110.9–50.9 mg liter^{-1} at the channel to 9.5–9.3 mg liter^{-1} at the landward side of the marsh. The investigators considered the water over the marsh to be low in nutrients, but the sediment to have sufficient quantities. The phosphorus concentrations decreased away from the sediment source in the same general pattern as found in the *Spartina townsendii* marsh studied by Ranwell (1964b).

Boyd (1969) noted that nutrient content of freshwater marsh plants is often quite high at the beginning of the growing season. He concluded that this might be the result of the plants storing available nutrients for use later in the growing season. This early growth and storage of nutrients occurs earlier than the optimum phytoplankton growth period, and may explain why phytoplankton crops are often reduced in lakes with extensive marshes.

The marshes along the polluted rivulet Lillån in Sweden also have high production due to high nutrient concentrations. The major emergent species present there are *Phragmites communis*, *Sparganium ramosum* and *Butomus umbellatus*. A loss of inorganic nitrogen and phosphorus in the Lillån was correlated with the rapid growth period of the marsh plants. During this period, the plants were removing nutrients from the soil solution. In order for the concentration of the nutrients in the sediment to be in equilibrium with the concentration in the stream, nutrients were removed from the water and incorporated by the sediment (Stake, 1967, 1968). In part, this correlation was not seen in the *Spartina alterniflora* marshes of Georgia because *S. alterniflora* removes nutrients from the deeper sediment layers, so that equilibration of the nutrient content of the sediments with that of the water occurs over a much longer time interval (Pomeroy *et al.*, 1969). In these salt marshes, the ultimate source of the nutrients is still the water flooding the marsh, but there is a net loss of produced material to the estuary, providing food for consumers there (Odum and de la Cruz, 1967; Reimold, 1965; Reimold and Daiber, 1970).

In some cases, nutrient concentrations in both water and sediment are important (Boyd, 1967). Moyle (1945, 1954) has found that water hardness affects species composition of freshwater marshes, while soil type affects their distribution. Boyd (1970c) found positive correlation between nutrient levels in plant tissue and in the water. However, elemental nutrient ratios in the plants are often different from those in the water, indicating that the plants actively take up the nutrients against a concentration gradient (Boyd, 1970d).

Another factor promoting high marsh production is the high concentration of organic matter in the soil leading to the formation of colloids. These absorb exchangeable ions necessary for plant growth (Albrecht, 1941; Gorham, 1953). The decomposition of organic matter produces large quantities of carbon dioxide, increasing the acidity of the water, and thereby increasing the solubility of iron and manganese. These ions may occur at concentrations that would normally be considered toxic (Robinson, 1930), but marsh plants have adapted to high concentrations and are able to take advantage of the other ions present (magnesium, phosphorus, calcium) in higher than normal concentrations. *Spartina* has an unusually high demand for iron (Teal and Teal, 1969).

NUTRIENT CONTENT OF MARSH PLANTS

Table 2 gives elemental ratios of various aquatic plants. C:N ratios are generally within the range of terrestrial plant C:N ratios of 30–40 (Alexander, 1961), but higher than C:N ratios of phytoplankton, perhaps due to a greater cellulose content in the marsh plants than in the phytoplankton.

N:P ratios are quite variable, due to environmental availability of nitrogen and phosphorus. Harper and Daniel (1934) noted that nitrogen concentrations in *Typha* are higher when grown in dark soil rich in organic matter, than in sandy soil, and that phosphorus content of marsh plants is higher than that of cultivated plants ordinarily used for forage. They concluded that the variation in phosphorus content of plants of the same species at different sites might be due to "luxury consumption" of this element when the plants are growing on fertile soils, since there was no indication of restriction of growth by nutrient depletion.

Marsh plant production, as well as nutrient content of the tissues, can reflect environmental nutrient availability. *Phragmites communis* can exhibit stunted growth as a result of nutrient deficient soil and water (Allen and Pearsall, 1963). Soil phosphorus can account for variation in *Typha latifolia* production (Boyd and Hess, 1970). Gerloff and Krombholz (1963) have used tissue analyses of some freshwater plants to determine nutrient availability. They found that the production in plant cultures with various nutrient concentrations in the water was correlated with nutrient content of the plant tissues when tissue nutrient concentrations were below certain critical levels. Above these levels, there was no correlation between production and environmental or tissue nutrient concentrations, thus indicating "luxury consumption.'

ENERGY FLOW

The primary producers of the marsh support two food webs. The primary consumers of the first are herbivores which feed on the standing marsh plants.

TABLE 2

Elemental composition of marsh plants

Species	Percent C	Percent N	Percent P	C:N (atomic)	N:P (atomic)	C:N:P (atomic)	Source
Spartina alterniflora	40.77	2.12	0.25	22.4	18.8	421:19:1	Burkholder (1956)
	....	0.54	...	...	...	.....	Taschdjian (1954)
	38.3	...	...	...	...	.....	Williams & Murdoch (1969)
	....	1.40	...	...	...	.....	Hall *et al.* (1970)
Spartina (dead at end of growing season)	46.69	1.60	...	34.0	...	.....	Odum & de la Cruz (1967)
Spartina alterniflora	46.32	3.68	...	14.7	...	.....	Odum & de la Cruz (1967)
(dead-partially decomposed)	....	0.16	...	...	...	.....	Hall *et al.* (1970)
Typha latifolia	....	1.4	0.17	...	18.2	.....	Harper & Daniel (1934)
	....	0.9	0.13	...	15.3	.....	Harper & Daniel (1934)
	....	2.3	0.14	...	36.4	.....	Harper & Daniel (1934)
	....	2.0	0.18	...	24.6	.....	Harper & Daniel (1934)
	....	3.6	0.30	...	26.6	.....	Harper & Daniel (1934)
	....	2.69	...	...	...	.....	Gorham (1953)
	44.9	1.59	0.18	33.0	20.0	645:20:1	Denton (1966)
Typha angustifolia	....	1.92	...	...	...	.....	Gorham (1953)
Sagittaria cuneata	....	2.25	0.22	...	22.6	.....	Harper & Daniel (1934)
	....	1.8	0.245	...	16.3	.....	Harper & Daniel (1934)
Sagittaria latifolia	....	2.04–2.91	...	...	...	.....	Boyd (1968)
	....	...	0.30	...	...	.....	Boyd (1970d)
Glyceria maxima	....	1.57	0.19	...	18.3	.....	Buttery *et al.* (1965)
	....	1.00	0.18	...	12.3	.....	Buttery *et al.* (1965)
Glyceria fluitans	....	2.75	...	...	...	.....	Gorham (1953)

TABLE 2—Continued

Elemental composition of marsh plants

Species	Percent C	Percent N	Percent P	C:N (atomic)	N:P (atomic)	C:N:P (atomic)	Source
Phragmites communis	....	1.76	0.12	...	32.5	.....	Buttery *et al.* (1965)
	....	1.56	0.14	...	24.7	.....	Buttery *et al.* (1965)
	....	1.80	0.17	...	23.4	.....	Stake (1967, 1968)
	....	0.90	0.08	...	24.9	.....	Stake (1967, 1968)
	....	0.65	0.05	...	28.8	.....	Stake (1967, 1968)
	....	1.88	0.17	...	24.5	.....	Allen & Pearsall (1963)
	....	1.59	0.07	...	50.3	.....	Allen & Pearsall (1963)
	....	2.04	0.15	...	30.1	.....	Allen & Pearsall (1963)
	....	1.30	0.03	...	96.0	.....	Allen & Pearsall (1963)
	....	1.60	0.10	...	35.4	.....	Allen & Pearsall (1963)
	....	2.11	0.12	...	38.9	.....	Allen & Pearsall (1963)
	....	2.70	0.15	...	39.9	.....	Allen & Pearsall (1963)
	....	3.57	...	...	...	.....	Gorham (1953)
Sparganium ramosum	....	3.29	0.60	...	12.1	.....	Stake (1967, 1968)
	....	1.98	0.45	...	9.7	.....	Stake (1967, 1968)
	....	1.70	0.36	...	10.5	.....	Stake (1967, 1968)
	....	2.22	0.25	...	19.7	.....	Stake (1967, 1968)
Sparganium simplex	....	3.40	0.42	...	17.9	.....	Stake (1967, 1968)
	....	2.06	0.40	...	11.4	.....	Stake (1967, 1968)
	....	1.41	0.24	...	13.0	.....	Stake (1967, 1968)
	....	1.41	0.21	...	14.1	.....	Stake (1967, 1968)
Sparganium erectum	....	1.30	...	...	...	.....	Gorham (1953)
Butomus umbellatus	....	3.36	0.75	...	9.9	.....	Stake (1967, 1968)
	....	2.36	0.57	...	9.2	.....	Stake (1967, 1968)
	....	1.90	0.46	...	9.1	.....	Stake (1967, 1968)
	....	1.50	0.32	...	10.4	.....	Stake (1967, 1968)

TABLE 2—Continued

Elemental composition of marsh plants

Species	Percent C	Percent N	Percent P	C:N (atomic)	N:P (atomic)	C:N:P (atomic)	Source
Juncus effusus	....	1.05	...	...	...	.....	Gorham (1953)
	....	...	0.27	...	...	.....	Boyd (1970d)
Eleocharis palustris	....	2.37	...	...	...	.....	Gorham (1953)
Juncus squarrosus (dead-partially decomposed)	42.06	1.39	...	35.4	...	.....	Latter & Cragg (1967)
Phalaris arundinacea	....	3.36	...	...	...	.....	Gorham (1953)
Molinia caerulea	....	2.61	...	...	...	.....	Gorham (1953)
	....	1.87	...	...	...	.....	Gorham (1953)
	....	2.40	...	...	...	.....	Gorham (1953)
Carex paniculata	....	2.32	...	...	...	.....	Gorham (1953)
Carex elata	....	1.87	...	...	...	.....	Gorham (1953)
Carex lasiocarpa	....	2.04	...	...	...	.....	Gorham (1953)
Carex canescens	....	1.42	...	...	...	.....	Gorham (1953)
Carex rostrata	....	1.72	...	...	...	.....	Gorham (1953)
Carex vesicaria	....	1.92	...	...	...	.....	Gorham (1953)
Manyanthes trifoliata	....	4.13	...	...	...	.....	Gorham (1953)
Calamogrostis lanceolata	....	2.76	...	...	...	.....	Gorham (1953)
Cladium mariscus	....	1.55	...	...	...	.....	Gorham (1953)
Justicia americana	....	2.0–3.6	...	...	...	.....	Boyd (1968)
	....	2.83	0.18	...	34.8	.....	Boyd (1969)
	....	1.63	0.09	...	40.1	.....	Boyd (1969)
Alternanthera philoxeroides	....	2.87	0.32	...	19.9	.....	Boyd (1969)

There are only a few consumer species in this web and they transform energy seasonally. These animals are most active during the summer and must reduce their activity during the winter when their food is unavailable. The primary consumers of the second web feed on the algae on the marsh floor and marsh plant detritus in the water and marsh floor. The energy flow of these populations is more constant through the year since detritus is produced continually, allowing development of an extensive web with many types of primary and secondary consumers. More dead grass is present in the colder months, but this is counterbalanced by the more rapid decomposition during the warmer months, so there is a continuous supply of food for consumers in this web (Odum and Smalley, 1959; Odum and de la Cruz, 1963).

The microbial fauna growing on the detritus produce necessary food for consumers. *Spartina alterniflora*, in particular, is somewhat nitrogen-poor. The bacteria growing on *Spartina* detritus remove dissolved nitrogen compounds from the water to produce protein, thereby increasing the protein content of the material taken by the consumers (Burkholder, 1956; Burkholder and Bornside, 1957; de la Cruz, 1965; Odum and de la Cruz, 1967). Other investigators (Hall, Weimer, and Lee, 1970) have found approximately the same quantity of protein in live *Spartina*, but less protein in the supposedly protein-rich, microbe-covered *Spartina* detritus than in the live plants. In this case, the detritus is of lower nutritive value to the consumers than the fresh *Spartina*. A similar pattern of covering bacteria has been found on *Thalassia testudinum* (Fenchel, 1970) and *Typhia latifolia* (Boyd, 1970a) detritus. Here, as in Burkholder's *Spartina* data, there was more protein in the detritus than in the living plants. Fenchel (1969, 1970) and Newell (1965) have observed that some detritus feeders remove the bacterial coating from the detritus and eliminate the harder to digest particles (e.g., cellulosic *Spartina* particles) in fecal pellets. These are then recolonized by bacteria and may be ingested again by the detritus feeders. Dissolved material released by decomposing *Spartina* particles is also utilized by bacteria (Ustach, 1969). Thus, some detritus feeders indirectly digest material from *Spartina* when they digest the bacteria that have fed on the dissolved substances released by decomposing *Spartina*.

A summary of energy flow in a Georgia salt marsh has been worked out by Teal (1962). Here *Spartina* accounts for ⅔ to ¾ of the primary production, while algae on the mud account for the rest (Pomeroy, 1959a, 1959b; Ragotskie, 1959; Schelske and Odum, 1961). The primary producers take up 6.1% of the incident radiation, but of their gross production 77% is utilized in their own respiration. This means that only 1.5% of the incident radiation is transformed into energy available to consumers. On a percentage basis, the energy conversion appears inefficient, but their is much vegetation produced and ample food available to form extensive food webs on the marsh and in the surrounding estuary. In other marshes, even less of the incident radiation is converted to organic matter. In a *Spartina alterniflora-Juncus roemerianus* marsh in oNrth Carolina, Stroud and Cooper (1969) found that only 0.2% of the incident radiation was converted to net primary production. Waits (1967) found 0.5% conversion in a North Carolina *Spartina patens-Juncus roemerianus* marsh. Bray (1962), work-

TABLE 3

Summary of Georgia salt marsh energetics (modified from Teal, 1962)

Gross primary production	6.1% of incident light
Producer respiration	77% of gross production
Bacterial respiration	47% of net production
Primary consumer respiration	7% of net production
Secondary consumer respiration	0.6% of net production
	55% of net production consumed on marsh
	45% of net production exported to estuary

ing in a *Typha angustifolia-latifolia* hybrid marsh in Minnesota, found that 0.6% of the incident light was utilized by the plants, but that much less of the gross production was consumed in plant respiration in the Minnesota marsh (15%) than in the Georgia marsh.

Table 3 summarizes Teal's energy flow diagram. Of the net primary production, 55% is consumed by the bacteria and other marsh consumers. This leaves 45% available for export to the estuary and consumption by the fauna there. The area of Georgia that he studied is 50% marsh and 50% open water. Of the total net primary production on an areal basis, including both marsh and open water, less than 10% is accounted for by phytoplankton production (Schelske and Odum, 1961). An input of 45% of the marsh production to the surrounding waters, therefore, provides much more net production to the estuarine consumers than would be available from phytoplankton production alone. The excellent adaptation of *Spartina* to this portion of the shoreline ecosystem is fortunate for the estuarine consumers. Without *Spartina*, their population might not be as extensive since no other plants have adapted as well to this rather hostile environment.

A study of net primary production of marsh plants (primarily *Spartina alterniflora*) and open water phytoplankton near Beaufort, North Carolina, has also been done (Williams, 1966; Williams and Murdoch, 1966, 1968, 1969). Here, the marsh accounts for only 5.9% of the estuarine area. However, marsh production accounts for 22.9% of the total net primary production. These investigators have not yet completed the energy flow relationships and measurements of export of material from the marsh to the estuary.

CONCLUSION

Extensive work has been done to determine net primary production of marsh communities. Their high production in comparison to terrestrial communities is well documented and the reasons for this high production have been described. The physical environment of the marsh is substantially different from the terrestrial environment. This seemingly hostile environment has been used to advantage by the marsh plants. Abundant water, the most obvious physical attribute of marshes, is of great importance to the high production of these plants. Water transports nutrients and maintains them in an ample, dissolved supply.

The impact of marshes on the flooding water is often great for in some ecosystems, the plants remove a large percentage of the nutrients in the water. The watery marsh environment also hastens the decomposition of organic matter and provides higher concentrations of iron, manganese and other ions which are needed by the plants. Hybrid vigor, leaf orientation, long growing season and other factors also play an important role in creating high production.

The consumer's utilization of salt marsh plant material has been widely studied. The plants support two food webs. The first web's primary consumers feed on the growing marsh plants. The primary consumers of the second web feed on the plants as detritus, both on the marsh floor and in the estuary. The populations of consumers supported to some extent by detritus are large and would be reduced by almost half in some estuaries if there were no input of detritus from salt marsh production.

The relative contribution of marsh detritus to freshwater ecosystems has not been determined, nor has the contribution of marsh detritus to a system like Chesapeake Bay been determined. In these systems, there are often three major sources of energy to consumers: 1) marsh detritus, 2) phytoplankton production, and 3) detritus from terrestrial sources, brought in by upland drainage. The extensively studied Georgia and North Carolina marsh ecosystems have only the first two sources. The functional significance of marshes in freshwater and Chesapeake-type ecosystems still needs to be determined. The energy relationships there are complex and the role of marshes may be somewhat variable. The phenomenon of reduced phytoplankton crops in lakes with extensive marshes indicates complex interactions between primary producers in these lacustrine ecosystems. The relative contributions of the various types of primary producers to the food supply may affect the populations of consumers and the energy flow patterns of the entire ecosystem.

LITERATURE CITED

ALBRECHT, W. A. 1941. Soil organic matter and ion availability for plants. *Soil Sci* **51**: 487–494.

ALEXANDER, MARTIN. 1961. *Introduction to Soil Microbiology*. J. Wiley & Sons, Inc.

ALLEN, S. E. and W. H. PEARSALL. 1963. Leaf analysis and shoot production in *Phragmites*. *Oikos*. **14**: 176–189.

AURAND, D. 1968. The seasonal and spatial distribution of nitrate and nitrite in the surface waters of two Delaware salt marshes. M. S. Thesis. Univ. Dela.

BAKER, J. M. 1970. Oil pollution in salt marsh communities. *Mar. Pollution Bul.* **1**(2): 27–28.

BLUM, J. L. 1969. Nutrient changes in water flooding the high salt marsh. *Hydrobiologia*. **34**: 95–99.

BOYD, C. E. 1967. Some aspects of aquatic plant ecology. *In Symposium on reservoir fishery resources*. Univ. of Georgia Press, Athens.

————. 1968. Freshwater plants: a potential source of protein. *Econ. Bot.* **22**: 359–368.

————. 1969. Production, mineral nutrient absorption, and biochemical assimilation by *Justicia americana* and *Alternanthera philoxeroides*. *Arch. Hydrobiol.* **66**: 139–160.

————. 1970a. Losses of mineral nutrients during decomposition of *Typha latifolia*. *Arch. Hydrobiol.* **66:** 511–517.

————. 1970b. Production, mineral accumulation and pigment concentrations in *Typha latifolia* and *Scirpus americanus*. *Ecology*. **51**(2): 285–290.

————. 1970c. Amino acid, protein and caloric content of vascular aquatic macrophytes. *Ecology*. **51:** 902–906.

————. 1970d. Chemical analyses of some vascular aquatic plants. *Arch. Hydrobiol.* **67:** 78–85.

————. and L. W. HESS. 1970. Factors influencing shoot production and mineral nutrient levels in *Typha latifolia*. *Ecology*. **51**(2): 296–300.

BRAY, J. R. 1962. Estimates of energy budgets for a *Typha* (cattail) marsh. *Science*. **136:** 1119–1120.

————, D. B. LAWRENCE and L. C. PEARSON. 1959. Primary production in some Minnesota terrestrial communities for 1957. *Oikos*. **10:** 38–49.

BURKHOLDER, P. R. 1956. Studies on the nutritive value of *Spartina* grass growing in the marsh areas of coastal Georgia. *Bull. Torrey bot. Club*. **83**(5): 327–334.

———— and G. H. BORNSIDE. 1957. Decomposition of marsh grass by aerobic marine bacteria. *Bull Torrey, bot. Club*. **84**:366–383.

BUTTERY, B. R., and J. M. LAMBERT. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. *J. Ecol.* **53:** 163–181.

————, W. T. WILLIAMS and J. M. LAMBERT. 1965. Competition between *Glyceria maxima* and *Phragmites communis* in the region of Surlingham Broad. II. The Fen Gradient. *J. Ecol.* **53:** 183–195.

CRUZ, A. A. DE LA. 1965. A study of particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. Ph.D. Thesis, Univ. of Georgia.

DENTON, JERRY B. 1966. Relationships between the chemical composition of aquatic plants and water quality. M.S. Auburn Univ.

FENCHEL, T. 1969. The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to ciliated protozoa. *Ophelia*. **6:** 1–182.

————. 1970. Studies on the decomposition of organic detritus derived from the turtle grass. *Thalassia testudinum*. *Limnol. Oceanogr.* **15**(1): 14–20.

FOSTER, W. A. 1968. Studies on the distribution and growth of *Juncus roemerianus* in southeastern Brunswick County, North Carolina. M. S. Thesis, North Carolina State Univ.

GERLOFF, G. C. and P. H. KROMBHOLZ. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. *Limnol. Oceanogr.* **11:** 529–537.

GOOCH, E. L. 1968. Hydrogen sulfide production and its effect on inorganic phosphate release from the sediments of the Canary Creek Marsh. M. A. Thesis, Univ. of Dela.

GOOD, R. E. 1965. Salt marsh vegetation, Cape May, New Jersey. *Bull. New Jersey Acad. Sci.* **10**(1): 1–11.

GORHAM, E. 1953. Chemical studies on the soils and vegetation of water-logged habitats in the English Lake District. *J. Ecol.* **41:** 345–360.

———— and W. H. PEARSALL. 1956. Production ecology: III. Shoot production in *Phragmites* in relation to habitat. *Oikos*. **7:** 206–214.

HALL, K. J., W. C. WEIMER and G. F. LEE. 1970. Amino acids in an estuarine environment. *Limnol. Oceanogr.* **15**(1): 162–164.

HARPER, H. J. and H. A. DANIEL. 1934. Chemical composition of certain aquatic plants. *Bot. Gaz.* **96:** 186–189.

HARPER, R. M. 1918. Some dynamic studies of Long Island vegetation. *Plant World.* **21:** 38–46.

HEALD, E. J. 1969. The production of organic detritus in a south Florida estuary. Ph. D. Thesis, Univ. of Miami.

HOESE, H. D. 1967. Effect of higher than normal salinites on salt marshes. *Contr. mar. Sci. Univ. Tex.* **12:**249–261.

HUBBARD, J. C. E. 1969. Light in relation to tidal immersion and growth of *Spartina townsendii* (s.l.) *J. Ecol.* **57:** 795–804.

JERVIS, R. A. 1964. Primary production in a freshwater marsh ecosystem. Ph.D. Thesis Rutgers Univ.

LAING, H. E. 1940a. Respiration of the rhizomes of *Nuphar advenum* and other aquatic plants. *Am. J. Bot.* **27**(7): 574–581.

————. 1940b. Respiration of the leaves of *Nuphar advenum* and *Typha latifolia. Am. J. Bot.* **27**(7): 583–586.

LATTER, P. M. and J. B. CRAGG. 1967. The decomposition of *Juncus squarrosus* leaves and microbiological changes in the profile of *Juncus* moor. *J. Ecol.* **55:** 465–481.

McNAUGHTON, S. J. 1966. Ecotype function in the *Typha* community-type. *Ecol. Monogr.* **36:** 297–325.

MORGAN, M. H. 1961. Annual angiosperm production on a salt mash. M .S. Thesis, Univ. Dela.

MOYLE, J. B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. *Am. Midl. Nat.* **34:** 402–420.

————. 1954. Some aspects of the chemistry of Minnesota surface waters as related to game and fish management. *Minn. Dept. of Cons., Div. of Game and Fish, Bur. of Fish., Invest. Rept. No. 151.*

NEWELL, R. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch, *Hydrobia ulvae,* and the bivalve, *Macoma balthica.* Proc. zool. Soc. Lond. **144:** 25–45.

ODUM, E. P. 1959. *Fundamentals of Ecology.* W. B. Saunders Co.

————. 1961. The role of tidal marshes in estuarin production. *N. Y. St. Conserv.* **15**(6): 12–15, 35.

———— and A. A. DE LA CRUZ. 1963. Detritus as a major component of ecosystems. *A.I.B.S. Bull.* **13**(3): 39–40.

———— and ————. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. *Estuaries AAAS* 383–388.

———— and A. E. SMALLEY. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in salt marsh ecosystem. *Proc. nat. Acad. Sci. U.S.* **45:** 617–622.

PALMER, E. L. 1941. Marshes and their environs. *Nature Mag.* **34:** 205–212.

PEARSALL, W. H. 1954. Growth and production. *Advmt. Sci.* **11:** 232–241.

———— and E. GORHAM. 1956. Production ecology. I. Standing crops of natural vegetation. *Oikos.* **7:** 193–201.

———— and P. J. NEWBOULD. 1957. Production ecology. IV. Standing crops of natural vegetation in the sub-arctic. *J. Ecol.* **45:** 593–599.

PENFOUND, W. T. 1956. Production of vascular aquatic plants. *Limnol. Oceanogr.* **1**(2): 92–101.

———— and T. T. EARLE. 1948. The biology of the water hyacinth. *Ecol. Monogr.* **18:** 447–472.

POMEROY, L. R. 1959a. Productivity of algae in salt marshes. *Proc. of Salt Marsh Conf., Mar. Inst., Univ. of Ga., Sapelo Isl., Ga.* 88–95.

————. 1959b. Algal productivity in salt marshes of Georgia. *Limnol. Oceanogr.* 4: 386–397.

————, R. E. JOHANNES, E. P. ODUM and B. ROFFMAN. 1969. The phosphorus and zinc cycles and productivity of the salt marsh. In *Proc. 2nd Natl. Symp. on Radioecology*. D. J. Nelson and F. C. Evans (ed.). 412–419.

————, E. E. SMITH and C. M. GRANT. 1965. The exchange of phosphate between estuarine water and sediments. *Limnol. Oceanogr.* **10:** 167–172.

RAGOTSKIE, R. A. 1959. Plankton productivity in estuarine waters of Georgia. *Publ. Inst. mar. Sci. Univ. Tex.* **6:** 146–158.

RANWELL, D. S. 1961. *Spartina* salt marshes in southern England. I. The effects of sheep grazing at the upper limits of *Spartina* marsh in Bridgwater Bay. *J. Ecol.* **49:** 325–340.

————. 1964a. *Spartina* salt marshes in southern England. II. Rate and seasonal pattern of sediment accretion. *J. Ecol.* **52:** 79–94.

————. 1964b. *Spartina* salt marshes in southern England. III. Rates of establishment, succession and nutrient supply at Bridgwater Bay, Somerset. *J. Ecol.* **52:** 95–105.

REIMOLD, R. J. 1965. An evaluation of inorganic phosphate concentrations of Canary Creek marsh. M.S. Thesis, Univ. of Dela.

———— and F. C. DAIBER. 1970. Dissolved phosphorus concentrations in a natural salt-marsh of Delaware. *Hydrobiologia.* **36:** 361–371.

ROBINSON, W .O. 1930. Some chemical phases of submerged soil conditions. *Soil Sci.* **30:** 197–217.

SCHELSKE, C. L. and E. P. ODUM. 1961, Mechanisms maintaining high productivity in Georgia Estuaries, *Proc. Gulf Caribb. Fish Inst.* **14:** 75–80.

SEIDEL, K. 1959. *Scirpus*-Kulturer. *Arch. Hydrobiol.* (*Plankt.*) **56:** 58–92.

SMALLEY, A. E. 1959. The growth cycle of *Spartina* and its relation to the insect populations in the marsh. *Proc. Salt Marsh Conf., Mar. Inst. Univ. of Ga., Sapelo Isl., Ga.* 96–100.

————. 1960. Energy flow of a salt marsh grasshopper population. *Ecology.* **41**(41): 672–677.

STAKE, E. 1967. Higher vegetation and nitrogen in a rivulet in central Sweden. *Schweiz. Z. Hydrol.* **29:** 107–124.

————. 1968. Higher vegetation and phosphorus in a small stream in central Sweden. *Schweiz. Z. Hydrol.* **30:** 353–373.

STROUD, L. M. and A. W. COOPER. 1969. Color-infrared aerial photographic interpretation and net primary productivity of a regularly-flooded North Carolina salt marsh. *Univ. of North Carolina, Water Resources Res. Inst., Rept. 14,* 86 p.

TASCHDJIAN, E. 1954. A note on *Spartina* protein. *Econ. Bot.* **8:** 164–165.

TEAL, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology.* **43:** 614–624.

———— and J. KANWISHER. 1966. Gas transport in the marsh grass, *Spartina alterniflora. J. Exp. Biol.* **17:** 355–361.

———— and MILDRED TEAL. 1969. *Life and death of a salt marsh.* Little, Brown and Co.

USTACH, J. F. 1969. The decomposition of *Spartina alterniflora.* M. S. Thesis, North Carolina State University.

WAITS, E. D. 1967. Net primary productivity of an irregularly-flooded North Carolina salt marsh. Ph.D. Dissert., North Carolina St. Univ.

WASS, M. L. and T. D. WRIGHT. 1969. Coastal wetlands of Virginia. Interim rept. to the Governor and General Assembly. *Virginia Inst. of Mar. Sci., Spec. Rept. in Applied Mar. Sci. and Ocean Eng. #10.*

WATSON, D. J. 1958. The dependence of net assimilation rate on leaf area index. *Ann. Bot.* **22:** 37–54.

WESTLAKE, D. F. 1963. Comparisons of plant productivity. *Biol. Rev.* **38:** 385–425.

————. 1965. Some basic data for investigations of the productivity of aquatic macrophytes. p. 229–248. *In: Primary Productivity in Aquatic Environments.* C. R. Goldman (ed.). Mem. Ist. Ital. Idrobiolo., 18 suppl., Univ. of Calif. Press, Berkeley.

————. 1966. The biomass and productivity of *Glyceria maxima.* I. Seasonal changes in biomass. *J. Ecol.* **54:** 745–753.

WILLIAMS, R. B. 1966. Annual phytoplankton production in a system of shallow temperate estuaries. p. 699–716. *In: Some Contemporary Studies in Marine Science.* H. Barnes (ed.). George Allen and Unwin. London.

———— and M. B. MURDOCH. 1966. Annual production of *Spartina alterniflora* and *Juncus roemerianus* in salt marshes near Beaufort, North Carolina. *ASB. Bulletin* **13:** 49.

————, and ————. 1968. Compartmental analysis of production and decay of *Juncus roemerianus. The ASB Bulletin* **15:** 59.

————, and ————. 1969. The potential importance of *Spartina alterniflora* in conveying zinc, manganese and iron into estuarine food chains. *In: Proc. 2nd Natl. Symp. on Radioecology.* D. J. Nelson and F. C. Ecans (ed.).

ACKNOWLEDGMENT

The author wishes to thank Drs. D. A. Flemer and D. H. Hamilton for editorial suggestions and Dr. R. B. Williams of the National Marine Fisheries Service, Beaufort, North Carolina, for pointing out additional references. Mrs. C. Essex, librarian, was very helpful in obtaining articles. This research was supported by Contract No. 14-01-0001-1979 with the United States Department of Interior, Office of Water Resources Research and is part of a project entitled, "The Effects of Thermal Loading and Water Quality on Estuarine Primary Production."

INSTRUCTIONS TO AUTHORS

1. Manuscripts should be sent to The Editor, Contributions in Marine Science, The University of Texas Marine Science Institute, Port Aransas, Texas 78373. Manuscripts may be submitted on any aspect of marine science. Preference is given to papers relating to the Gulf of Mexico and presenting the results of original research. Papers describing new methods will also be considered. Reviews may be published but authors should consult with the editor before submitting a manuscript. Reviews will normally be considered from workers active in the field reviewed.

   Papers will be returned to the authors for revision if the style and presentation does not conform to the journal's conventions.

2. The submission of a manuscript will be taken to imply that it has not already been published nor is being considered for publication and, if accepted by *Contributions in Marine Science,* that it will not be published elsewhere.

3. Manuscripts must be typewritten in English with double spacing throughout.

4. Page one of the manuscript should give the title in capitals, the author's name and the address(es) where the work was carried out. Footnotes may be used on the title page to indicate present addresses of authors, but should be avoided in the main text. Also included on page one should be a short title of not more than 60 letters and spaces for use as a page heading.

5. Page two should contain an abstract. This should be concise and intelligible without the need to refer to the text.

6. The introduction should start on page three. The major headings (ABSTRACT, INTRODUCTION, MATERIALS AND METHODS, RESULTS, DISCUSSION) should be capitalized and centered in the page. For sub-headings, capitalize the initial letter of significant words. The first subheading should be centered, the second shouldered and the third run-on with the text.

7. Use metric units instead of or in addition to other units. Authors should consult *Style Manual for Biological Journals* The American Institute of Biological Sciences, Washington, D. C. for questions of general style and a list of acceptable abbreviations.

8. References in the text may be in the form "Smith (1960)" or "(Smith 1960)". When repeated reference is made to papers with more than two authors, give the authors in full the first time and subsequently use the first author followed by *et al.* The full list of authors should be listed under literature cited. When reference is made to a book, the page may be indicated in the text, *e.g.* (Smith 1960, p. 170).

9. The literature cited should be arranged alphabetically by author(s) and then chronologically, i.e., Smith, A. and Abe, B. 1970. comes before Smith, A. and Brown, A. 1960. The titles of papers are given in full; the title of journals may be abbreviated according to the *World List of Scientific Periodicals, 4th Edition.* The titles of obscure journals should be given in full.

10. References to books should give the author or editor, date, title, page, publisher's name and place of publication. The following examples illustrate the style to be followed:

    Journal:

    VAN CLEVE, R., R. Y. TING and J. C. KENT. 1966. A new device for sampling marine demersal animals for ecological studies. *Limnol. Oceanogr.* **11:** 438–443.

    Book:

    HUTCHINSON, J. 1959. *Families of Flowering Plants.* Macmillan, N. Y. 792 p.

    Thesis:

    HOESE, H. D. 1965. Spawning of marine fishes in the Port Aransas, Texas area as determined by the distribution of young and larvae. Ph.D. Thesis, Univ. of Texas, Austin.

    Chapter:

    PROVASOLI, L. 1963. Organic regulation of phytoplankton fertility, p. 165–210. In M. N. Hill (ed.) *The Sea, Vol. 2.* Interscience, N. Y.

11. Line drawings on Bristol Board or good quality white paper should be drawn large enough for reproduction to ½ size. They should not exceed 11 x 8½ inches.
12. Photographs should be on glossy paper. The names of authors, the number of the illustration and an indication of the top edge should be given on the reverse of all illustrations. Legends to the figures and tables should be typed on a separate sheet of paper.
13. There are no page charges but the high cost of printing may preclude the acceptance of long papers with large numbers of illustrations unless the author can make a contribution to the cost of publication.